

Cockroach

Cockroaches are insects of the order Blattodea, which also includes termites. About 30 cockroach species out of 4,600 are associated with human habitats. About four species are well known as pests.

The cockroaches are an ancient group, dating back at least as far as the Carboniferous period, some 320 million years ago. Those early ancestors however lacked the internal ovipositors of modern roaches. Cockroaches are somewhat generalized insects without special adaptations like the sucking mouthparts of aphids and other true bugs; they have chewing mouthparts and are likely among the most primitive of living neopteran insects. They are common and hardy insects, and can tolerate a wide range of environments from Arctic cold to tropical heat. Tropical cockroaches are often much bigger than temperate species, and, contrary to popular belief, extinct cockroach relatives and 'roachoids' such as the Carboniferous *Archimylacris* and the Permian *Apthoroblattina* were not as large as the biggest modern species.

Some species, such as the gregarious German cockroach, have an elaborate social structure involving common shelter, social dependence, information transfer and kin recognition. Cockroaches have appeared in human culture since classical antiquity. They are popularly depicted as dirty pests, though the great majority of species are inoffensive and live in a wide range of habitats around the world.

Contents

Taxonomy and evolution

Description

Distribution and habitat

Behavior

- Collective decision-making
- Social behavior
- Sounds

Biology

- Digestive tract
- Tracheae and breathing
- Reproduction
- Hardiness

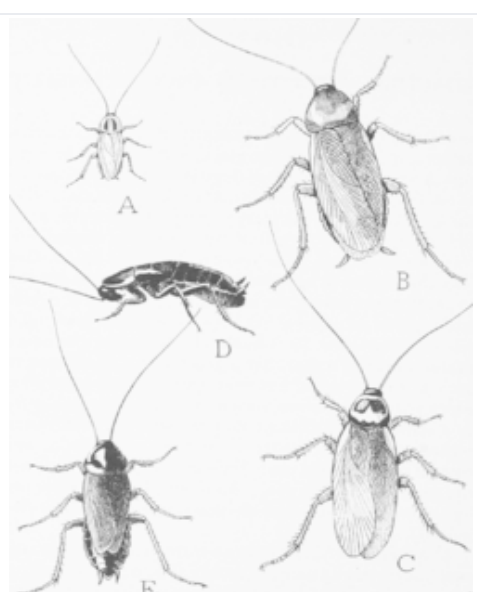
Relationship with humans

- In research and education
- As pests
 - Control
- As food
- In traditional and homeopathic medicine
- Conservation

Cultural depictions

References

External links

Cockroach									
Temporal range: 145–0 Ma									
PreЄ	Є	OS	D	C	P	T	J	K	PgN
Cretaceous–recent									
									
Common household cockroaches									
A) German cockroach									
B) American cockroach									
C) Australian cockroach									
D&E) Oriental cockroach (♀ & ♂)									
Scientific classification									
Kingdom:		Animalia							
Phylum:		Arthropoda							
Class:		Insecta							
Superorder:		Dictyoptera							
Order:		Blattodea							
Families									
Blaberidae									
Blattidae									
Corydiidae									
Cryptocercidae									
Ectobiidae									
Lamproblattidae									
Nocticolidae									
Tryonicidae									

Taxonomy and evolution



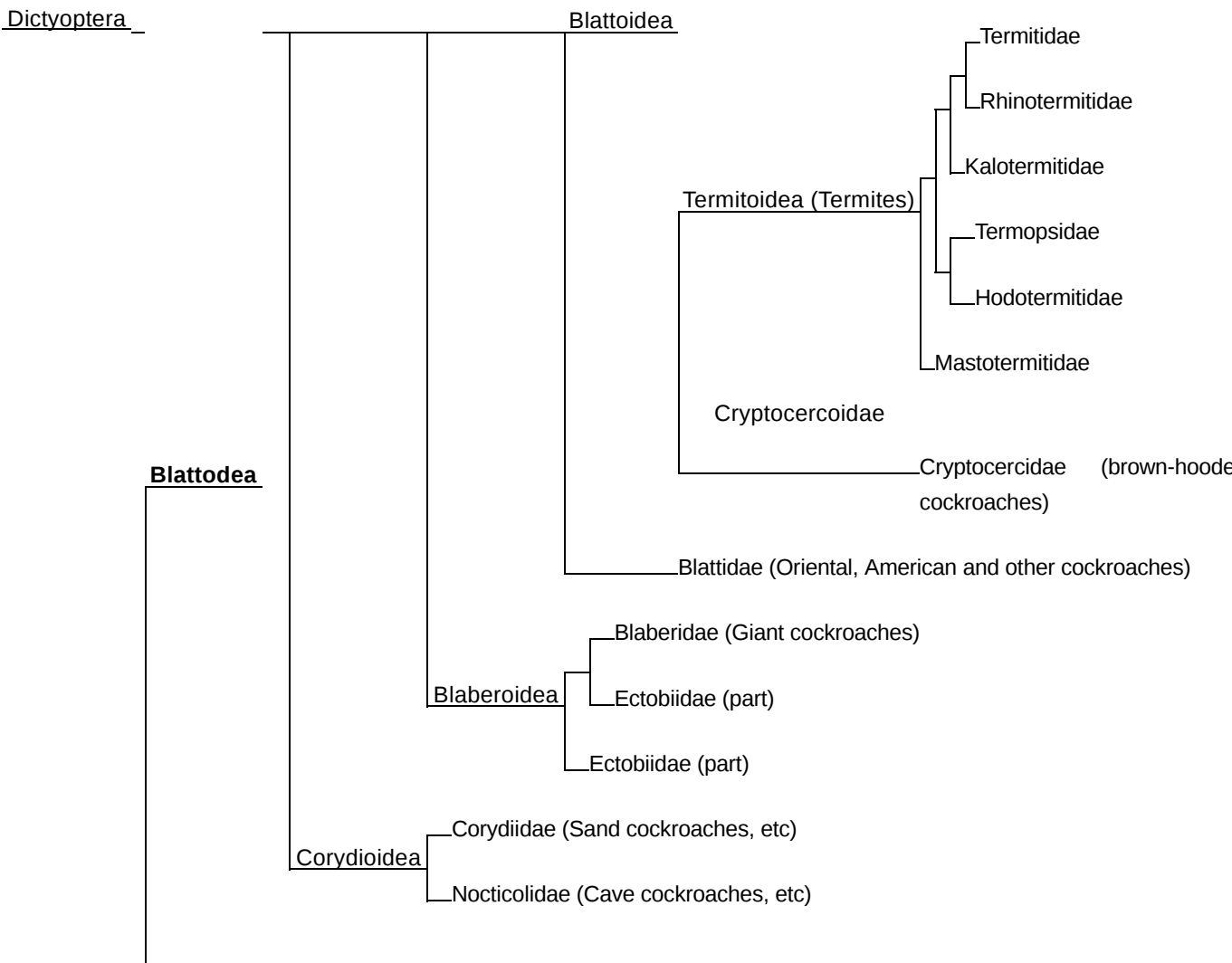
A 40- to 50-million-year-old cockroach in Baltic amber (Eocene)

Cockroaches are members of the order Blattodea, which includes the termites, a group of insects once thought to be separate from cockroaches. Currently, 4,600 species and over 460 genera are described worldwide.^{[1][2]} The name "cockroach" comes from the Spanish word for cockroach, *cucaracha*, transformed by 1620s English folk etymology into "cock" and "roach".^[3] The scientific name derives from the Latin *blatta*, "an insect that shuns the light", which in classical Latin was applied to not only cockroaches, but also mantids.^{[4][5]}

Historically, the name Blattaria was used largely interchangeably with the name Blattodea, but whilst the former name was used to refer to 'true' cockroaches exclusively, the latter also includes the termites. The current catalogue of world cockroach species uses the name Blattodea for the group.^[1] Another name, Blattoptera, is also sometimes used.^[6] The earliest cockroach-like fossils ("blattopterans" or "roachids") are from the Carboniferous period 320 million years ago, as are fossil roachoid nymphs.^{[7][8][9]}

Since the 19th century, scientists believed that cockroaches were an ancient group of insects that had a Devonian origin, according to one hypothesis.^[10] Fossil roachoids that lived during that time differ from modern cockroaches in having long external ovipositors and are the ancestors of mantises, as well as modern blattodeans. As the body, hind wings and mouthparts are not preserved in fossils frequently, the relationship of these roachoids and modern cockroaches remains disputed. The first fossils of modern cockroaches with internal ovipositors appeared in the early Cretaceous. A recent phylogenetic analysis suggests that cockroaches originated at least in the Jurassic.^[10]

The evolutionary relationships of the Blattodea (cockroaches and termites) shown in the cladogram are based on Eggleton, Beccaloni & Inward (2007).^[11] The cockroach families Lamproblattidae and Tryonicidae are not shown but are placed within the superfamily Blattoidea. The cockroach families Corydiidae and Ectobiidae were previously known as the Polyphagidae and Blattellidae.^[12]



Termites were previously regarded as a separate order Isoptera to cockroaches. However, recent genetic evidence strongly suggests that they evolved directly from 'true' cockroaches, and many authors now place them as an "epifamily" of Blattodea.^[11] This evidence supported a hypothesis suggested in 1934 that termites are closely related to the wood-eating cockroaches (genus *Cryptocercus*). This hypothesis was originally based on similarity of the symbiotic gut flagellates in termites regarded as living fossils and wood-eating cockroaches.^[13] Additional evidence emerged when F. A. McKittrick (1965) noted similar morphological characteristics between some termites and cockroach nymphs.^[14] The similarities among these cockroaches and termites have led some scientists to reclassify termites as a single family, the Termitidae, within the order Blattodea.^{[11][15]} Other scientists have taken a more conservative approach, proposing to retain the termites as the Termitoidea, an epifamily within the order. Such measure preserves the classification of termites at family level and below.^[16]

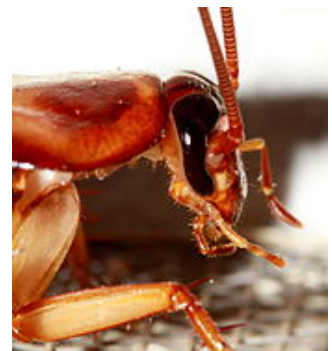
Description



Domino cockroach *Therea petiveriana*, normally found in India

Most species of cockroach are about the size of a thumbnail, but several species are bigger. The world's heaviest cockroach is the Australian giant burrowing cockroach *Macropanesthia rhinoceros*, which can reach 9 cm (3.5 in) in length and weigh more than 30 g (1.1 oz).^[17] Comparable in size is the Central American giant cockroach *Blaberus giganteus*, which grows to a similar length.^[18] The longest cockroach species is *Megaloblatta longipennis*, which can reach 97 mm (3.8 in) in length and 45 mm (1.8 in) across.^[19] A Central and South American species, *Megaloblatta blaberoides*, has the largest wingspan of up to 185 mm (7.3 in).^[20]

Cockroaches are generalized insects, with few special adaptations, and may be among the most primitive living neopteran insects. They have a relatively small head and a broad, flattened body, and most species are reddish-brown to dark brown. They have large compound eyes, two ocelli, and long, flexible antennae. The mouthparts are on the underside of the head and include generalized chewing mandibles, salivary glands and various touch and taste receptors.^[21]



Head of *Periplaneta americana*

The body is divided into a thorax of three segments and a ten-segmented abdomen. The external surface has a tough exoskeleton which contains calcium carbonate and protects the inner organs and provides attachment to muscles. It is coated with wax to repel water. The wings are attached to the second and third thoracic segments. The tegmina, or first pair of wings, are tough and protective, lying as a shield on top of the membranous hind wings, which are used in flight. All four wings have branching longitudinal veins, and multiple cross-veins.^[22]

The three pairs of legs are sturdy, with large coxae and five claws each.^[22] They are attached to each of the three thoracic segments. The front legs are the shortest and the hind legs the longest, providing the main propulsive power when the insect runs.^[21] The spines on the legs were earlier considered to be sensory, but observations of the insect's gait on sand and wire meshes have demonstrated that they help in locomotion on difficult terrain. The structures have been used as inspiration for robotic legs.^{[23][24]}

The abdomen has ten segments, each with a pair of spiracles for respiration. Segment ten bears a pair of cerci, a pair of anal styles, the anus and the external genitalia. Males have an aedeagus through which they secrete sperm during copulation and females have spermathecae for storing sperm and an ovipositor through which the ootheca is laid.^[21]

Distribution and habitat

Cockroaches are abundant throughout the world and live in a wide range of environments, especially in the tropics and subtropics.^[25] Cockroaches can withstand extremely cold temperatures, allowing them to live in the Arctic. Some species are capable of surviving temperatures of -188°F (-122°C) by manufacturing an antifreeze made out of glycerol.^[26] In North America, 50 species separated into

five families are found throughout the continent.^[25] 450 species are found in Australia.^[27] Only about four widespread species are commonly regarded as pests.^{[28][29]}

Cockroaches occupy a wide range of habitats. Many live in leaf litter, among the stems of matted vegetation, in rotting wood, in holes in stumps, in cavities under bark, under log piles and among debris. Some live in arid regions and have developed mechanisms to survive without access to water sources. Others are aquatic, living near the surface of water bodies, including bromeliad phytotelmata, and diving to forage for food. Most of these respire by piercing the water surface with the tip of the abdomen which acts as a snorkel, but some carry a bubble of air under their thoracic shield when they submerge. Others live in the forest canopy where they may be one of the main types of invertebrate present. Here they may hide during the day in crevices, among dead leaves, in bird and insect nests or among epiphytes, emerging at night to feed.^[30]

Behavior

Cockroaches are social insects; a large number of species are either gregarious or inclined to aggregate, and a slightly smaller number exhibit parental care.^[31] It used to be thought that cockroaches aggregated because they were reacting to environmental cues, but it is now believed that pheromones are involved in these behaviors. Some species secrete these in their feces with gut microbial symbionts being involved, while others use glands located on their mandibles. Pheromones produced by the cuticle may enable cockroaches to distinguish between different populations of cockroach by odor. The behaviors involved have been studied in only a few species, but German cockroaches leave fecal trails with an odor gradient.^[31] Other cockroaches follow such trails to discover sources of food and water, and where other cockroaches are hiding. Thus, cockroaches have emergent behavior, in which group or swarm behavior emerges from a simple set of individual interactions.^[32]

Daily rhythms may also be regulated by a complex set of hormonal controls of which only a small subset have been understood. In 2005, the role of one of these proteins, pigment dispersing factor (PDF), was isolated and found to be a key mediator in the circadian rhythms of the cockroach.^[33]

Pest species adapt readily to a variety of environments, but prefer warm conditions found within buildings. Many tropical species prefer even warmer environments. Cockroaches are mainly nocturnal^[34] and run away when exposed to light. An exception to this is the Asian cockroach, which flies mostly at night but is attracted to brightly lit surfaces and pale colors.^[35]



A cockroach soon after ecdysis

Collective decision-making

Gregarious cockroaches display collective decision-making when choosing food sources. When a sufficient number of individuals (a "quorum") exploits a food source, this signals to newcomer cockroaches that they should stay there longer rather than leave for elsewhere.^[36] Other mathematical models have been developed to explain aggregation dynamics and conspecific recognition.^{[37][38]}

Cooperation and competition are balanced in cockroach group decision-making behavior.^[32]

Cockroaches appear to use just two pieces of information to decide where to go, namely how dark it is and how many other cockroaches there are. A study used specially-scented roach-sized robots that appear to the roaches as real to demonstrate that once there are enough insects in a place to form a critical mass, the roaches accepted the collective decision on where to hide, even if this was an unusually lit place.^[39]

Social behavior

When reared in isolation, German cockroaches show behavior that is different from behavior when reared in a group. In one study, isolated cockroaches were less likely to leave their shelters and explore, spent less time eating, interacted less with conspecifics when exposed to them, and took longer to recognize receptive females. Because these changes occurred in many contexts, the authors suggested them as constituting a behavioral syndrome. These effects might have been due either to reduced metabolic and developmental rates in isolated individuals or the fact that the isolated individuals hadn't had a training period to learn about what others were like via their antennae.^[40]

Individual American cockroaches appear to have consistently different "personalities" regarding how they seek shelter. In addition, group personality is not simply the sum of individual choices, but reflects conformity and collective decision-making.^{[41][42]}

The gregarious German and American cockroaches have elaborate social structure, chemical signalling, and "social herd" characteristics. Lihoreau and his fellow researchers stated:^[32]

“ The social biology of domiciliary cockroaches ... can be characterized by a common shelter, overlapping generations, non-closure of groups, equal reproductive potential of group members, an absence of task specialization, high levels of social dependence, central place foraging, social information transfer, kin recognition, and a meta-population structure.^[32] ”

Sounds

Some species make a hissing noise while other cockroaches make a chirping noise. The Madagascar hissing cockroach produces its sound through the modified spiracles on the fourth abdominal segment. Several different hisses are produced, including disturbance sounds, produced by adults and larger nymphs; and aggressive, courtship and copulatory sounds produced by adult males.^[43] *Henschoutedenia epilamproides* has a stridulatory organ between its thorax and abdomen, but the purpose of the sound produced is unclear.^[44]

Several Australian species practice acoustic and vibration behavior as an aspect of courtship. They have been observed producing hisses and whistles from air forced through the spiracles. Furthermore, in the presence of a potential mate, some cockroaches tap the substrate in a rhythmic, repetitive manner. Acoustic signals may be of greater prevalence amongst perching species, particularly those that live on low vegetation in Australia's tropics.^[45]

Biology

Digestive tract

Cockroaches are generally omnivorous; the American cockroach (*Periplaneta americana*), for example, feeds on a great variety of foodstuffs including bread, fruit, leather, starch in book bindings, paper, glue, skin flakes, hair, dead insects and soiled clothing.^[46] Many species of cockroach harbor in their gut symbiotic protozoans and bacteria which are able to digest cellulose. In many species, these symbionts may be essential if the insect is to utilize cellulose; however, some species secrete cellulase in their saliva, and the wood-eating cockroach, *Panesthia cribrata*, is able to survive indefinitely on a diet of crystallized cellulose while being free of micro-organisms.^[47]

The similarity of these symbionts in the genus *Cryptocercus* to those in termites are such that these cockroaches have been suggested to be more closely related to termites than to other cockroaches,^[48] and current research strongly supports this hypothesis about their relationships.^[49] All species studied so far carry the obligate mutualistic endosymbiont bacterium *Blattabacterium*, with the exception of *Nocticola australiense*, an Australian cave-dwelling species without eyes, pigment or wings, which recent genetic studies indicate is a very primitive cockroach.^{[50][51]} It had previously been thought that all five families of cockroach were descended from a common ancestor that was infected with *B. cuenoti*. It may be that *N. australiense* subsequently lost its symbionts, or alternatively this hypothesis will need to be re-examined.^[51]

Tracheae and breathing

Like other insects, cockroaches breathe through a system of tubes called tracheae which are attached to openings called spiracles on all body segments. When the carbon dioxide level in the insect rises high enough, valves on the spiracles open and carbon dioxide diffuses out and oxygen diffuses in. The tracheal system branches repeatedly, the finest tracheoles bringing air directly to each cell, allowing gaseous exchange to take place.^[52]

While cockroaches do not have lungs as do vertebrates, and can continue to respire if their heads are removed, in some very large species, the body musculature may contract rhythmically to forcibly move air in and out of the spiracles; this may be considered a form of breathing.^[52]

Reproduction

Cockroaches use pheromones to attract mates, and the males practice courtship rituals, such as posturing and stridulation. Like many insects, cockroaches mate facing away from each other with their genitalia in contact, and copulation can be prolonged. A few species are known to be parthenogenetic, reproducing without the need for males.^[22]

Female cockroaches are sometimes seen carrying egg cases on the end of their abdomens; the German cockroach holds about 30 to 40 long, thin eggs in a case called an ootheca. She drops the capsule prior to hatching, though live births do occur in rare instances. The egg capsule may take more than five hours to lay and is initially bright white in color. The eggs are hatched from the combined pressure of the hatchlings gulping air. The hatchlings are initially bright white nymphs and continue inflating themselves with air, becoming harder and darker within about four hours. Their transient white stage while hatching and later while molting has led to claims of albino cockroaches.^[22] Development from eggs to adults takes three to four months. Cockroaches live up to a year, and the female may produce up to eight egg cases in a lifetime; in favorable conditions, she can produce 300 to 400 offspring. Other species of cockroaches, however, can produce far more eggs; in some cases a female needs to be impregnated only once to be able to lay eggs for the rest of her life.^[22]

The female usually attaches the egg case to a substrate, inserts it into a suitably protective crevice, or carries it about until just before the eggs hatch. Some species, however, are ovoviviparous, keeping the eggs inside their body, with or without an egg case, until they hatch. At least one genus, *Diploptera*, is fully viviparous.^[22]

Cockroaches have incomplete metamorphosis, meaning that the nymphs are generally similar to the adults, except for undeveloped wings and genitalia. Development is generally slow, and may take a few months to over a year. The adults are also long-lived, and have survived for as much as four years in the laboratory.^[22]



3 millimeter
cockroach nymph



Female *Periplaneta
fuliginosa* with
ootheca



Empty ootheca



American
cockroach oothecae

Hardiness

Cockroaches are among the hardiest insects. Some species are capable of remaining active for a month without food and are able to survive on limited resources, such as the glue from the back of postage stamps.^[53] Some can go without air for 45 minutes. Japanese cockroach (*Periplaneta japonica*) nymphs, which hibernate in cold winters, survived twelve hours at -5°C to -8°C in laboratory experiments.^[54]

Experiments on decapitated specimens of several species of cockroach found a variety of behavioral functionality remained, including shock avoidance and escape behavior, although many insects other than cockroaches are also able to survive decapitation, and popular claims of the longevity of headless cockroaches do not appear to be based on published research.^{[55][56]} The severed head is able to survive and wave its antennae for several hours, or longer when refrigerated and given nutrients.^[56]

It is popularly suggested that cockroaches will "inherit the earth" if humanity destroys itself in a nuclear war. Cockroaches do indeed have a much higher radiation resistance than vertebrates, with the lethal dose perhaps six to 15 times that for humans. However, they are not exceptionally radiation-resistant compared to other insects, such as the fruit fly.^[57]

The cockroach's ability to withstand radiation better than human beings can be explained through the cell cycle. Cells are most vulnerable to the effects of radiation when they are dividing. A cockroach's cells divide only once each time it molts, which is weekly at most in a juvenile roach. Since not all cockroaches would be molting at the same time, many would be unaffected by an acute burst of radiation, although lingering radioactive fallout would still be harmful.^[52]

Relationship with humans

In research and education

Because of their ease of rearing and resilience, cockroaches have been used as insect models in the laboratory, particularly in the fields of neurobiology, reproductive physiology and social behavior.^[31] The cockroach is a convenient insect to study as it is large and simple to raise in a laboratory environment. This makes it suitable both for research and for school and undergraduate biology studies. It can be used in experiments on topics such as learning, sexual pheromones, spatial orientation, aggression, activity rhythms and the biological clock, and behavioral ecology.^[58] Research conducted in 2014 suggests that humans fear cockroaches the most, even more than mosquitoes, due to an evolutionary aversion.^[59]



Cockroaches in research:
Periplaneta americana in an
electrophysiology experiment

As pests

The Blattodea include some thirty species of cockroaches associated with humans; these species are atypical of the thousands of species in the order.^[60] They feed on human and pet food and can leave an offensive odor.^[61] They can passively transport pathogenic microbes on their body surfaces, particularly in environments such as hospitals.^{[62][63]} Cockroaches are linked with allergic reactions in humans.^{[64][65]} One of the proteins that trigger allergic reactions is tropomyosin.^[66] These allergens are also linked with asthma.^[67] About 60% of asthma patients in Chicago are also sensitive to cockroach allergens. Studies similar to this have been done globally and all the results are similar. Cockroaches can live for a few days up to a month without food, so just because no cockroaches are visible in a home does not mean they are not there. Approximately 20-48% of homes with no visible sign of cockroaches have detectable cockroach allergens in dust.^[68]

Cockroaches can burrow into human ears, causing pain and hearing loss.^{[69][70]} They may be removed with forceps, possibly after first drowning with olive oil.^{[71][72][73]}

Control

Many remedies have been tried in the search for control of the major pest species of cockroaches, which are resilient and fast-breeding. Household chemicals like sodium bicarbonate (baking soda) have been suggested, without evidence for their effectiveness.^[74] Garden herbs including bay, catnip, mint, cucumber, and garlic have been proposed as repellents.^[75] Poisoned bait containing hydramethylnon or fipronil, and boric acid powder is effective on adults.^[76] Baits with egg killers are also quite effective at reducing the cockroach population. Alternatively, insecticides containing deltamethrin or pyrethrin are very effective.^[76] In Singapore and Malaysia, taxi drivers use pandan leaves to repel cockroaches in their vehicles.^[77]

Few parasites and predators are effective for biological control of cockroaches. Parasitoidal wasps such as *Ampulex* wasps sting nerve ganglia in the cockroach's thorax, temporarily paralyzing the victim, allowing the wasp to deliver an incapacitating sting into the cockroach's brain. The wasp clips the antennae with its mandibles and drinks some hemolymph before dragging the prey to a burrow, where an egg (rarely two) is laid on it.^[78] The wasp larva feeds on the subdued living cockroach.^{[79][80]} Another wasp which is considered a promising candidate for biological control is the ensign wasp *Evania appendigaster* which attacks cockroach oothecae to lay a single egg inside.^{[81][82]} Ongoing research is still developing technologies allowing for mass-rearing these wasps for application releases.^{[83][84]}

Cockroaches can be trapped in a deep, smooth-walled jar baited with food inside, placed so that cockroaches can reach the opening, for example with a ramp of card or twigs on the outside. An inch or so of water or stale beer (by itself a cockroach attractant) in the jar can be used to drown any insects thus captured. The method works well with the American cockroach, but less so with the German cockroach.^[85]

A study conducted by scientists at Purdue University concluded that the most common cockroaches in the US, Australia and Europe were able to develop a “cross resistance” to multiple types of pesticide. This contradicted previous understanding that the animals can develop resistance against one pesticide at a time.^[86] The scientists suggested that cockroaches will no longer be easily controlled using a diverse spectrum of chemical pesticides and that a mix of other means, such as traps and better sanitation, will need to be employed.^[87]

As food

Although considered disgusting in Western culture, cockroaches are eaten in many places around the world.^{[88][89]} Whereas household pest cockroaches may carry bacteria and viruses, cockroaches bred under laboratory conditions can be used to prepare nutritious food.^[90] In Mexico and Thailand, the heads and legs are removed, and the remainder may be boiled, sautéed, grilled, dried or diced.^[88] In China, cockroaches have become popular as medicine and cockroach farming is rising with over 100 farms.^[91] The cockroaches are fried twice in a wok of hot oil, which makes them crispy with soft innards that are like cottage cheese.^{[92][93]} Fried cockroaches are ground and sold as pills for stomach, heart and liver diseases.^[94] A cockroach recipe from Formosa (Taiwan) specifies salting and frying cockroaches after removing the head and entrails.^[95]

In traditional and homeopathic medicine

In China, cockroaches are raised in large quantities for medicinal purposes.^[96]

Two species of cockroach were used in homeopathic medicine in the 19th century.^[97]

Conservation

While a small minority of cockroaches are associated with human habitats and viewed as repugnant by many people, a few species are of conservation concern. The Lord Howe Island wood-feeding cockroach (*Panesthia lata*) is listed as endangered by the New South Wales Scientific Committee, but the cockroach may be extinct on Lord Howe Island itself. The introduction of rats, the spread of Rhodes grass (*Chloris gayana*) and fires are possible reasons for their scarcity.^[98] Two species are currently listed as endangered and critically endangered by the IUCN Red List, *Delosia ornata* and *Nocticola gerlachi*.^{[99][100]} Both cockroaches have a restricted distribution and are threatened by habitat loss and rising sea levels. Only 600 *Delosia ornata* adults and 300 nymphs are known to exist, and these are threatened by a hotel development. No action has been taken to save the two cockroach species, but protecting their natural habitats may prevent their extinction. In the former Soviet Union, cockroach populations have been declining at an alarming rate; this may be exaggerated, or the phenomenon may be temporary or cyclic.^[101] One species of roach, *Simandoa conserfariam*, is considered extinct in the wild.

Cultural depictions

Cockroaches were known and considered repellent but useful in medicines in Classical times. An insect named in Greek "σίλφη" (*silphe*) has been identified with the cockroach. It is mentioned by Aristotle, saying that it sheds its skin; it is described as foul-smelling in Aristophanes' play *Peace*; Euenus called it a pest of book collections, being "page-eating, destructive, black-bodied" in his *Analect*. Virgil named the cockroach "Lucifuga" ("one that avoids light"). Pliny the Elder recorded the use of "Blatta" in various medicines; he describes the insect as disgusting, and as seeking out dark corners to avoid the light.^{[102][103]} Dioscorides recorded the use of the "Silphe", ground up with oil, as a remedy for earache.^[103]

Lafcadio Hearn (1850–1904) asserted that "For tetanus cockroach tea is given. I do not know how many cockroaches go to make up the cup; but I find that faith in this remedy is strong among many of the American population of New Orleans. A poultice of boiled cockroaches is placed over the wound." He adds that cockroaches are eaten, fried with garlic, for indigestion.^[104]

Several cockroach species, such as *Blaptica dubia*, are raised as food for insectivorous pets.^[105] A few cockroach species are raised as pets, most commonly the giant Madagascar hissing cockroach, *Gromphadorhina portentosa*.^[106] Whilst the hissing cockroaches may be the most commonly kept species, there are many species that are kept by cockroach enthusiasts; there is even a specialist society: the Blattodea Culture Group (BCG), which was a thriving organisation for about 15 years although now appears to be dormant.^[107] The BCG provided a source of literature for people interested in rearing cockroaches which was otherwise limited to either scientific papers, or general insect books, or books covering a variety of exotic pets; in the absence of an inclusive book one member published *Introduction to Rearing Cockroaches* which still appears to be the only book dedicated to rearing cockroaches.^[108]



Madagascar hissing cockroaches kept as pets

Cockroaches have been used for space tests. A cockroach given the name Nadezhda was sent into space by Russian scientists as part of a Foton-M mission, during which she mated, and later became the first terrestrial animal to produce offspring that had been conceived in space.^[109]

Because of their long association with humans, cockroaches are frequently referred to in popular culture. In Western culture, cockroaches are often depicted as dirty pests.^{[110][111]} In a 1750–1752 journal, Peter Osbeck noted that cockroaches were frequently seen and found their way to the bakeries, after the sailing ship *Gothenburg* ran aground and was destroyed by rocks.^[112]

Donald Harington's satirical novel *The Cockroaches of Stay More* (Harcourt, 1989) imagines a community of "roosterroaches" in a mythical Ozark town where the insects are named after their human counterparts. Madonna has famously quoted, "I am a survivor. I am like a cockroach, you just can't get rid of me."^[113] An urban legend maintains that cockroaches are immortal.^[114]

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Housefly

The **housefly** (*Musca domestica*) is a fly of the suborder Cyclorrhapha. It is believed to have evolved in the Cenozoic era, possibly in the Middle East, and has spread all over the world as a commensal of humans. It is the most common fly species found in houses. Adults are grey to black, with four dark, longitudinal lines on the thorax, slightly hairy bodies, and a single pair of membranous wings. They have red eyes, set farther apart in the slightly larger female.

The female housefly usually mates only once and stores the sperm for later use. She lays batches of about 100 eggs on decaying organic matter such as food waste, carrion, or feces. These soon hatch into legless white larvae, known as maggots. After 2 to 5 days of development, these metamorphose into reddish-brown pupae, about 8 mm (0.3 in) long. Adult flies normally live for 2 to 4 weeks, but can hibernate during the winter. The adults feed on a variety of liquid or semiliquid substances, as well as solid materials which have been softened by their saliva. They can carry pathogens on their bodies and in their faeces, contaminate food, and contribute to the transfer of food-borne illnesses, while, in numbers, they can be physically annoying. For these reasons, they are considered pests.

Houseflies have been used in the laboratory in research into aging and sex determination. Flies appear in literature from Ancient Greek myth and Aesop's *The Impertinent Insect* onwards. Authors sometimes choose the fly to speak of the brevity of life, as in William Blake's 1794 poem "The Fly", which deals with mortality subject to uncontrollable circumstances.

Contents

Description
Distribution
Evolution and taxonomy
Life cycle
Ecology
Relationship with humans
As a disease vector
In warfare
In waste management
Control
In science
In literature
References
Further reading
External links


Description



Head of a female housefly with two large compound eyes and three ocelli

Adult houseflies are usually 6 to 7 mm (0.24 to 0.28 in) long with a wingspan of 13 to 15 mm (0.5 to 0.6 in). The females tend to be larger winged than males, while males have relatively longer legs. Females tend to vary more in size^[1] and there is geographic variation with larger individuals in higher latitudes.^[2] The head is strongly convex in front and flat and slightly conical behind. The pair of large compound eyes almost touch in the male, but are more widely separated in the female. They have three simple eyes (ocelli) and a pair of short antennae.^[3] Flies process visual information around seven times more quickly than humans, enabling them to identify and avoid attempts to catch or swat them, since they effectively see the human's movements in slow motion with their higher flicker fusion rate.^{[4][5]}

The mouthparts are specially adapted for a liquid diet; the mandibles and maxillae are reduced and not functional, and the other mouthparts form a retractable, flexible proboscis with an enlarged, fleshy tip, the labellum. This is a sponge-like structure that is characterised by many grooves, called pseudotracheae, which suck up fluids by capillary action.^{[6][7]} It is also used to distribute saliva to soften solid foods or collect loose particles.^[8] Houseflies have chemoreceptors, organs of taste, on the tarsi of their legs, so they can identify foods such as sugars by walking over them.^[9] Flies are often seen cleaning their legs by rubbing them together, enabling the chemoreceptors to taste afresh whatever they walk on next.^[10] At the end of each leg is a pair of claws, and below them are two adhesive pads, pulvilli, enabling the fly to walk up smooth walls and ceilings using Van der Waals forces. The claws help the fly to unstick the foot for the next step. Flies walk with a common gait on horizontal and vertical surfaces with three legs in contact with the surface and three in movement. On inverted surfaces, they alter the gait to keep four feet stuck to the surface.^[11] Flies land on a ceiling by flying straight towards it; just before landing, they make a half roll and point all six legs at the surface, absorbing the shock with the front legs and sticking a moment later with the other four.^[12]

Housefly	
 <div></div> 	
Conservation status	
<i>Not evaluated</i> (IUCN 3.1)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Diptera
Section:	Schizophora
Family:	Muscidae
Genus:	<i>Musca</i>
Species:	<i>M. domestica</i>
Binomial name	
<i>Musca domestica</i> <div>Linnaeus, 1758</div>	
Subspecies	
<div> <ul style="list-style-type: none"> <i>M. d. calleva</i> Walker, 1849 <i>M. d. domestica</i> Linnaeus, 1758 </div>	



Mouthparts, showing the pseudotracheae, semitubular grooves (dark parallel bands) used for sucking up liquid food



Wing, under 250x magnification

The thorax is a shade of gray, sometimes even black, with four dark, longitudinal bands of even width on the dorsal surface. The whole body is covered with short hairs. Like other Diptera, houseflies have only one pair of wings; what would be the hind pair is reduced to small halteres that aid in flight stability. The wings are translucent with a yellowish tinge at their base. Characteristically, the medial vein (M1+2 or fourth long vein) shows a sharp upward bend. Each wing has a lobe at the back, the calypter, covering the haltere. The abdomen is gray or yellowish with a dark stripe and irregular dark markings at the side. It has 10 segments which bear spiracles for respiration. In males, the ninth segment bears a pair of claspers for copulation, and the 10th bears anal cerci in both sexes.^{[3][13]}

A variety of species around the world appear similar to the housefly, such as the lesser house fly, *Fannia canicularis*; the stable fly, *Stomoxys calcitrans*;^[13] and other members of the genus *Musca* such as *M. vetustissima*, the Australian bush fly and several closely related taxa that include *M. primitiva*, *M. shanghaiensis*, *M. violacea*, and *M. varenensis*.^[14]



Micrograph of tarsus of leg, showing claws and bristles including the central one between the two pulvilli known as the empodium

The systematic identification of species may require the use of region-specific taxonomic keys and can require dissections of the male reproductive parts for confirmation.^{[15][16]}

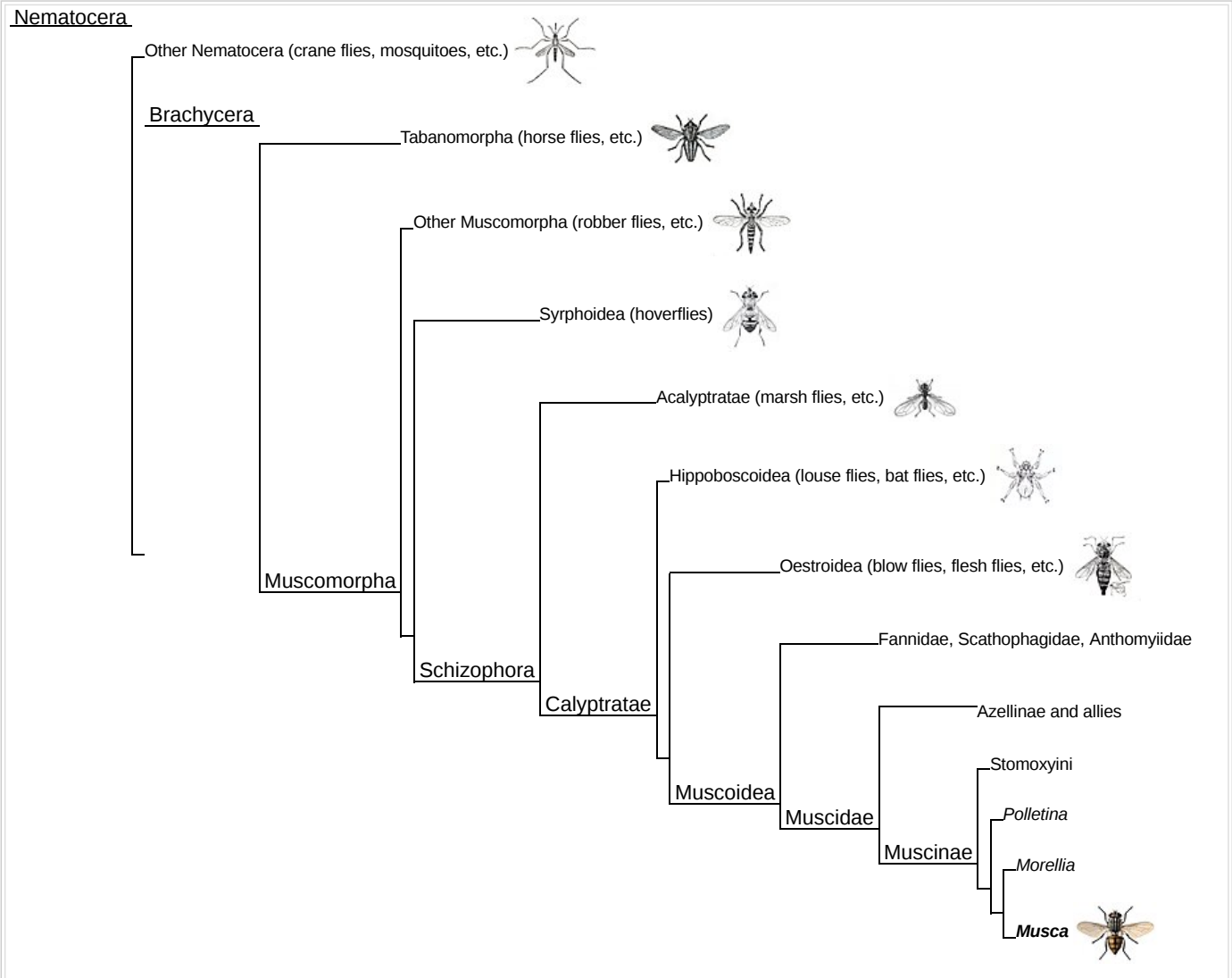
Distribution

The housefly is probably the insect with the widest distribution in the world; it is largely associated with humans and has accompanied them around the globe. It is present in the Arctic, as well as in the tropics, where it is abundant. It is present in all populated parts of Europe, Asia, Africa, Australasia, and the Americas.^[3]

Evolution and taxonomy

Though the order of flies (Diptera) is much older, true houseflies are believed to have evolved in the beginning of the Cenozoic era.^[17] The housefly's superfamily, Muscoidea, is most closely related to the Oestroidea (blow flies, flesh flies and allies), and more distantly to the Hippoboscoidea (louse flies, bat flies and allies). They are thought to have originated in the southern Palearctic region, particularly the Middle East. Because of their close, commensal relationship with humans, they probably owe their worldwide dispersal to co-migration with humans.^[18]

The housefly was first described as *Musca domestica* in 1758 based on the common European specimens by the Swedish botanist and zoologist Carl Linnaeus in his *Systema naturae* and continues to be classified under that name.^[19] A more detailed description was given in 1776 by the Danish entomologist Johan Christian Fabricius in his *Genera Insectorum*.^[3]



Life cycle



Houseflies mating

14 °C (57 °F).^[13]

When metamorphosis is complete, the adult fly emerges from the pupa. To do this, it uses the ptilinum, an eversible pouch on its head, to tear open the end of the pupal case. The adult housefly lives from two weeks to a month in the wild, or longer in benign laboratory conditions. Having emerged from the pupa, it ceases to grow; a small fly is not necessarily a young fly, but is instead the result of getting insufficient food during the larval stage.^[13]

Male houseflies are sexually mature after 16 hours and females after 24. Females produce a pheromone, (Z)-9-tricosene (muscalure). This cuticular hydrocarbon is not released into the air and males sense it only on contact with females;^[12] it has found use as in pest control, for luring males to fly traps.^{[24][25]} The male initiates the mating by bumping into the female, in the air or on the ground, known as a "strike". He climbs on to her thorax, and if she is receptive, a courtship period follows, in which the female vibrates her wings and the male strokes her head. The male then reverses onto her abdomen and the female pushes her ovipositor into his genital opening; copulation, with sperm transfer, lasts for several minutes. Females normally mate only once and then reject further advances from males, while males mate multiple times.^[26] A volatile semiochemical that is deposited by females on their eggs attracts other gravid females and leads to clustered egg deposition.^[27]

The larvae depend on warmth and sufficient moisture to develop; generally, the warmer the temperature, the faster they grow. In general, fresh swine and chicken manures present the best conditions for the developing larvae, reducing the larval period and increasing the size of the pupae. Cattle, goat, and horse manures produce fewer, smaller pupae, while fully composted swine manure, with a water content under 40%, produces none at all.^[28] Pupae can range from about 8.0 to 20 milligrams (0.0003 to 0.0007 ounces) under different conditions.^[29]

The lifecycle can be completed in seven to 10 days under optimal conditions, but may take up to two months in adverse circumstances. In temperate regions, 12 generations may occur per year, and in the tropics and subtropics, more than 20.^[13]

Ecology



Housefly pupae killed by parasitoid wasp larvae: Each pupa has one hole through which a single adult wasp has emerged; the wasp larvae fed on the housefly larvae.

Houseflies play an important ecological role in breaking down and recycling organic matter. Adults are mainly carnivorous; their primary food is animal matter, carrion, and faeces, but they also consume milk, sugary substances, and rotting fruit and vegetables. Solid foods are softened with saliva before being sucked up.^[7] They can be opportunistic blood feeders.^[30] Houseflies have a mutualistic relationship with the bacterium *Klebsiella oxytoca*, which can live on the surface of housefly eggs and deter fungi which compete with the fly larvae for nutrients.^[31]

Adult houseflies are diurnal and rest at night. If inside a building after dark, they tend to congregate on ceilings, beams, and overhead wires, while out of doors, they crawl into foliage or long grass, or rest in shrubs and trees or on wires.^[13] In cooler climates, some houseflies hibernate in winter, choosing to do so in cracks and crevices, gaps in woodwork, and the folds of curtains. They arouse in the spring when the weather warms up, and search out a place to lay their eggs.^[32]

Houseflies have many predators, including birds, reptiles, amphibians, various insects, and spiders. The eggs, larvae, and pupae have many species of stage-specific parasites and parasitoids. Some of the more important are the parasitic wasps *Muscidifurax uniraptor* and *Spalangia cameroni*; these lay their eggs in the fly larvae tissue and their offspring complete their development before the adult flies can emerge from the pupae.^[13] Hister beetles feed on housefly larvae in manure heaps and the predatory mite

Macrocheles muscae domesticae consumes housefly eggs, each mite eating 20 eggs per day.^[33]

Houseflies sometimes carry phoretic (nonparasitic) passengers, including mites such as *Macrocheles muscaedomesticae*^[34] and the pseudoscorpion *Lamprochernes chyzeri*.^[35]

The pathogenic fungus *Entomophthora muscae* causes a fatal disease in houseflies. After infection, the fungal hyphae grow throughout the body, killing the fly in about five days. Infected flies have been known to seek high temperatures that could suppress the growth of the fungus. Affected females tend to be more attractive to males, but the fungus-host interactions have not been fully understood.^[36] The housefly also acts as the alternative host to the parasitic nematode *Habronema muscae* that attacks horses.^[37]

Relationship with humans



Larva and adult, by Amedeo John Engel Terzi (1872–1956)

Flies are a nuisance, disturbing people at leisure and at work, but they are disliked principally because of their habits of contaminating foodstuffs. They alternate between breeding and feeding in dirty places with feeding on human foods, during which process they soften the food with saliva and deposit their feces, creating a health hazard.^[38] However, fly larvae are as nutritious as fish meal, and could be used to convert waste to feed for fish and livestock.^[39]

Flies have been used in art and artefacts in many cultures. In 16th- and 17th-century European vanitas paintings, flies sometimes occur as *memento mori*. They may also be used for other effects as in the Flemish painting, the *Master of Frankfurt* (1496). Fly amulets were popular in ancient Egypt.^{[40][41]}

As a disease vector



Housefly lapping up food from a plate

Houseflies can fly for several miles from their breeding places,^[42] carrying a wide variety of organisms on their hairs, mouthparts, vomitus, and faeces. Parasites carried include cysts of protozoa, e.g. *Entamoeba histolytica* and *Giardia lamblia* and eggs of helminths, e.g., *Ascaris lumbricoides*, *Trichuris trichiura*, *Hymenolepis nana*, and *Enterobius vermicularis*.^[43] Houseflies do not serve as a secondary host or act as a reservoir of any bacteria of medical or veterinary importance, but they do serve as mechanical vectors to over 100 pathogens, such as those causing typhoid, cholera, salmonellosis,^[44] bacillary dysentery,^[45] tuberculosis, anthrax, ophthalmia,^[46] and pyogenic cocci, making them especially problematic in hospitals and during outbreaks of certain diseases.^[43] Disease-causing organisms on the outer surface of the fly may survive for a few hours, but those in the crop or gut can be viable for several days.^[38] Usually, too few bacteria are on the external surface of the flies (except perhaps for *Shigella*) to cause infection, so the main routes to human infection are through the fly's regurgitation and defecation.^[47]

In the early 20th century, Canadian public health workers believed that the control of flies was important in controlling the spread of tuberculosis. A "swat that fly" contest was held for children in Montreal in 1912.^[48] Flies were targeted in 1916, when a polio epidemic broke out in the eastern United States. The belief that fly control was key to disease control continued, with extensive use of insecticidal spraying, well until the mid-1950s, declining only after the introduction of Salk's vaccine.^[49] In China, Mao Zedong's Four Pests Campaign between 1958 and 1962 exhorted the people to catch and kill flies, along with rats, mosquitoes and sparrows.^[50]

In warfare

During the Second World War, the Japanese worked on entomological warfare techniques under Shirō Ishii. Japanese Yagi bombs developed at Pingfan consisted of two compartments, one with houseflies and another with a bacterial slurry that coated the flies prior to release. *Vibrio cholerae*, which causes cholera, was the bacterium of choice, and was used in China in Baoshan in 1942, and in northern Shandong in 1943. Baoshan had been used by the Allies and bombing produced epidemics that killed 60,000 people in the initial stages reaching a radius of 200 km, which finally took a toll of 200,000 victims. The Shandong attack killed 210,000; the occupying Japanese troops had been vaccinated in advance.^[51]

In waste management

The ability of housefly larvae to feed and develop in a wide range of decaying organic matter is important for recycling of nutrients in nature. This could be exploited to combat ever-increasing amounts of waste.^[52] Housefly larvae can be mass-reared in a controlled manner in animal manure, reducing the bulk of waste and minimizing environmental risks of its disposal.^{[53][54]} Harvested maggots may be used as feed for animal nutrition.^{[54][55]}

Control



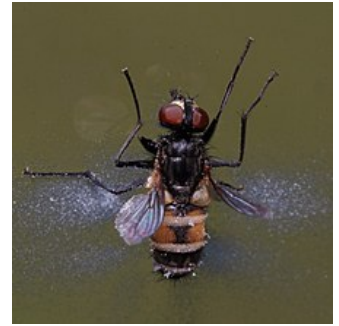
Detail of a 1742 painting by Frans van der Mijl that uses a fly in a Renaissance allegory of touch theme

Flies can be controlled, at least to some extent, by physical, chemical, or biological means. Physical controls include screening with small mesh or the use of vertical strips of plastic or strings of beads in doorways to prevent entry of flies into buildings. Fans to create air movement or air barriers in doorways can deter flies from entering, and food premises often use fly-killing devices; sticky fly papers hanging from the ceiling are effective,^[47] but electric "bug zappers" should not be used directly above food-handling areas because of scattering of contaminated insect parts.^[56] Another approach is the elimination as far as possible of potential breeding sites. Keeping garbage in lidded containers and collecting it regularly and frequently, prevents any eggs laid from developing into adults. Unhygienic rubbish tips are a prime fly-breeding site, but if garbage is covered by a layer of soil, preferably daily, this can be avoided.^[47]

Insecticides can be used. Larvicides kill the developing larvae, but large quantities may need to be used to reach areas below the surface. Aerosols can be used in buildings to "zap" flies, but outside applications are only temporarily effective. Residual sprays on walls or resting sites have a longer-lasting effect.^[47] Many strains of housefly have become immune to the most commonly used insecticides.^{[57][58]}

Several means of biological pest control have been investigated. These include the introduction of another species, the black soldier fly (*Hermetia illucens*), whose larvae compete with those of the housefly for resources.^[59] The introduction of dung beetles to churn up the surface of a manure heap and render it unsuitable for breeding is another approach.^[59] Augmentative biological control by releasing parasitoids can be used, but flies breed so fast that the natural enemies are unable to keep up.^[60]

In science



Housefly killed by the pathogenic fungus *Entomophthora muscae*



Philadelphia Department of Health poster warning the public of fly hazards (c. 1942)

The ease of culturing houseflies, and the relative ease of handling them when compared to the fruit fly *Drosophila*, have made them useful as model organism for use in laboratories. The American entomologist Vincent Dethier, in his humorous *To Know A Fly* (1962), pointed out that as a laboratory animal, houseflies did not trouble anyone sensitive to animal cruelty. Houseflies have a small number of chromosomes, haploid six or diploid 12.^[61] Because the somatic tissue of the housefly consists of long-lived postmitotic cells, it can be used as an informative model system for understanding cumulative age-related cellular alterations. Oxidative DNA damage 8-hydroxydeoxyguanosine in houseflies was found in one study to increase with age and reduce life expectancy supporting the hypothesis that oxidative molecular damage is a causal factor in senescence (aging).^{[62][63][64]}

The housefly is an object of biological research, partly for its variable sex-determination mechanism. Although a wide variety of sex-determination mechanisms exists in nature (e.g. male and female heterogamy, haplodiploidy, environmental factors), the way sex is determined is usually fixed within a species. The housefly is, however, thought to exhibit multiple mechanisms for sex determination, such as male heterogamy (like most insects and mammals), female heterogamy (like birds), and maternal control over offspring sex. This is because a male-determining gene (*Mdmd*) can be found on most or all housefly chromosomes.^[65] Sexual differentiation is controlled as in other insects by an ancient developmental switch, doublesex, which is regulated by the transformer protein in many different insects.^[66] *Mdmd* causes male development by negatively regulating *transformer*. There is also a female-determining allele of *transformer* that is not sensitive to the negative regulation of *Mdmd*.^[67]

The antimicrobial peptides produced by housefly maggots are of pharmacological interest.^[68]

In the 1970s, the aircraft modeller Frank Ehling constructed miniature balsa-wood aircraft powered by live houseflies.^[69] Studies of tethered flies have helped in the understanding of insect vision, sensory perception, and flight control.^[70]



William Blake's illustration of "The Fly" in *Songs of Innocence and of Experience*, 1794

In literature

The Impertinent Insect is a group of five fables, sometimes ascribed to Aesop, concerning an insect, in one version a fly, which puffs itself up to seem important. In the Biblical fourth plague of Egypt, flies represent death and decay, while the Philistine god Beelzebub's name may mean "lord of the flies".^[71] In Greek mythology, Myiagros was a god who chased away flies during the sacrifices to Zeus and Athena; Zeus sent a fly to bite Pegasus, causing Bellerophon to fall back to Earth when he attempted to ride the winged steed to Mount Olympus.^[72] In the traditional Navajo religion, Big Fly is an important spirit being.^{[73][74][75]}

William Blake's 1794 poem "The Fly", part of his collection *Songs of Experience*, deals with the insect's mortality, subject to uncontrollable circumstances, just like humans.^[76] Emily Dickinson's 1855 poem "I Heard a Fly Buzz When I Died" speaks of flies in the context of death.^[77] In William Golding's 1954 novel *Lord of the Flies*, the fly is however a symbol of the children involved.^[78]

Ogden Nash's humorous two-line 1942 poem "God in His wisdom made the fly/And then forgot to tell us why." indicates the debate about the value of biodiversity, given that even those considered by humans as pests have their place in the world's ecosystems.^[79]

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Cricket (insect)

Crickets (also known as "**true crickets**"), of the family **Gryllidae**, are insects related to bush crickets, and, more distantly, to grasshoppers. The Gryllidae have mainly cylindrical bodies, round heads, and long antennae. Behind the head is a smooth, robust pronotum. The abdomen ends in a pair of long cerci; females have a long, cylindrical ovipositor. The hind legs have enlarged femora, providing power for jumping. The front wings are adapted as tough, leathery elytra, and some crickets chirp by rubbing parts of these together. The hind wings are membranous and folded when not in use for flight; many species, however, are flightless. The largest members of the family are the bull crickets, *Brachytrupes*, which are up to 5 cm (2 in) long.

More than 900 species of crickets are described; the Gryllidae are distributed all around the world except at latitudes 55° or higher, with the greatest diversity being in the tropics. They occur in varied habitats from grassland, bushes, and forests to marshes, beaches, and caves. Crickets are mainly nocturnal, and are best known for the loud, persistent, chirping song of males trying to attract females, although some species are mute. The singing species have good hearing, via the tympana on the tibiae of the front legs.

Crickets often appear as characters in literature. The Talking Cricket features in Carlo Collodi's 1883 children's book, *The Adventures of Pinocchio*, and in films based on the book. The eponymous insect is central to Charles Dickens's 1845 *The Cricket on the Hearth*, as is the chirping insect in George Selden's 1960 *The Cricket in Times Square*. Crickets are celebrated in poems by William Wordsworth, John Keats, and Du Fu. They are kept as pets in countries from China to Europe, sometimes for cricket fighting. Crickets are efficient at converting their food into body mass, making them a candidate for food production. They are used as human food in Southeast Asia, where they are sold deep-fried in markets as snacks. They are also used to feed carnivorous pets and zoo animals. In Brazilian folklore, crickets feature as omens of various events.

Contents

- Description
- Distribution and habitat
- Biology
 - Defence
 - Chirping
 - Flight
 - Diet
 - Reproduction and lifecycle

Cricket

Temporal range: Triassic–Recent

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Juvenile *Gryllus campestris*

Scientific classification

Kingdom:

Animalia

Phylum:

Arthropoda

Class:

Insecta

Order:

Orthoptera

Suborder:

Ensifera

Superfamily:

Grylloidea

Family:

Gryllidae

Laicharting, 1781^[2]

Subfamilies

See Taxonomy section

Synonyms^[2]

■

Gryllides Laicharting, 1781

Inbreeding avoidance
Predators, parasites, and pathogens

■ *Paragryllidae* Desutter-Grandcolas, 1987

Phylogeny and taxonomy

Subfamilies

In human culture

Folklore and myth
In literature
As pets and fighting animals
As food
Common expressions
In popular culture

Notes

References

Further reading

External links

Description



African field cricket *Gryllus bimaculatus*

Crickets are small to medium-sized insects with mostly cylindrical, somewhat vertically flattened bodies. The head is spherical with long slender antennae arising from cone-shaped scapes (first segments) and just behind these are two large compound eyes. On the forehead are three ocelli (simple eyes). The pronotum (first thoracic segment) is trapezoidal in shape, robust, and well-sclerotinized. It is smooth and has neither dorsal or lateral keels (ridges).^[3]

At the tip of the abdomen is a pair of long cerci (paired appendages on rearmost segment), and in females, the ovipositor is cylindrical, long and narrow, smooth and shiny. The femora (third segments) of the back pair of legs are greatly enlarged for jumping. The tibiae (fourth segments) of the hind legs are armed with a number of moveable spurs, the arrangement of which is characteristic of each species. The tibiae of the front legs bear one or more tympani which are used for the reception of sound.^[3]

The wings lie flat on the body and are very variable in size between species, being reduced in size in some crickets and missing in others. The fore wings are elytra made of tough chitin, acting as a protective shield for the soft parts of the body and in males, bear the stridulatory organs for the production of sound. The hind pair is membranous, folding fan-wise under the fore wings. In many species, the wings are not adapted for flight.^[1]

The largest members of the family are the 5 cm (2 in)-long bull crickets (*Brachytrupes*) which excavate burrows a metre or more deep. The tree crickets (Oecanthinae) are delicate white or pale green insects with transparent fore wings, while the field crickets (Gryllinae) are robust brown or black insects.^[1]

Distribution and habitat

Crickets have a cosmopolitan distribution, being found in all parts of the world with the exception of cold regions at latitudes higher than about 55° North and South. They have colonised many large and small islands, sometimes flying over the sea to reach these locations, or perhaps conveyed on floating timber or by human activity. The greatest diversity occurs in tropical locations,

such as in Malaysia, where 88 species were heard chirping from a single location near Kuala Lumpur. A greater number than this could have been present because some species are mute.^[1]

Crickets are found in many habitats. Members of several subfamilies are found in the upper tree canopy, in bushes, and among grasses and herbs. They also occur on the ground and in caves, and some are subterranean, excavating shallow or deep burrows. Some make home in rotting wood, and certain beach-dwelling species can run and jump over the surface of water.^[1]

Biology

Defence

Crickets are relatively defenceless, soft-bodied insects. Most species are nocturnal and spend the day hidden in cracks, under bark, inside curling leaves, under stones or fallen logs, in leaf litter, or in the cracks in the ground that develop in dry weather. Some excavate their own shallow holes in rotting wood or underground and fold in their antennae to conceal their presence. Some of these burrows are temporary shelters, used for a single day, but others serve as more permanent residences and places for mating and laying eggs. Crickets burrow by loosening the soil with the mandibles and then carrying it with the limbs, flicking it backwards with the hind legs or pushing it with the head.^[4]

Other defensive strategies are the use of camouflage, fleeing, and aggression. Some species have adopted colourings, shapes, and patterns that make it difficult for predators that hunt by sight to detect them. They tend to be dull shades of brown, grey, and green that blend into their background, and desert species tend to be pale. Some species can fly, but the mode of flight tends to be clumsy, so the most usual response to danger is to scuttle away to find a hiding place.^[4]

Chirping

Most male crickets make a loud chirping sound by stridulation (scraping two specially textured limbs together). The stridulatory organ is located on the tegmen, or fore wing, which is leathery in texture. A large vein runs along the centre of each tegmen, with comb-like serrations on its edge forming a file-like structure, and at the rear edge of the tegmen is a scraper. The tegmina are held at an angle to the body and rhythmically raised and lowered which causes the scraper on one wing to rasp on the file on the other. The central part of the tegmen contains the "harp", an area of thick, sclerotized membrane which resonates and amplifies the volume of sound, as does the pocket of air between the tegmina and the body wall. Most female crickets lack the necessary adaptations to stridulate, so make no sound.^[5]

Several types of cricket songs are in the repertoire of some species. The calling song attracts females and repels other males, and is fairly loud. The courting song is used when a female cricket is near and encourages her to mate with the caller. A triumphal song is produced for a brief period after a successful mating, and may reinforce the mating bond to encourage the female to lay some eggs rather than find another male.^[6] An aggressive song is triggered by contact chemoreceptors on the antennae that detect the presence of another male cricket.^[7]

Crickets chirp at different rates depending on their species and the temperature of their environment. Most species chirp at higher rates the higher the temperature is (about 62 chirps a minute at 13 °C (55 °F) in one common species; each species has its own rate). The relationship between temperature and the rate of chirping is known as Dolbear's law. According to this law, counting



A male *Gryllus* cricket chirping: Its head faces its burrow; the leathery fore wings (tegmina; singular "tegmen") are raised (clear of the more delicate hind wings) and are being scraped against each other (stridulation) to produce the song. The burrow acts as a resonator, amplifying the sound.

the number of chirps produced in 14 seconds by the snowy tree cricket, common in the United States, and adding 40 will approximate the temperature in degrees Fahrenheit.^[6]

In 1975, Dr. William H. Cade discovered that the parasitic tachinid fly *Ormia ochracea* is attracted to the song of the cricket, and uses it to locate the male to deposit her larvae on him. It was the first known example of a natural enemy that locates its host or prey using the mating signal.^[8] Since then, many species of crickets have been found to be carrying the same parasitic fly, or related species. In response to this selective pressure, a mutation leaving males unable to chirp was observed amongst a population of *Teleogryllus oceanicus* on the Hawaiian island of Kauai, enabling these crickets to elude their parasitoid predators.^[9] A different mutation with the same effect was also discovered on the neighboring island of Oahu (ca. 100 miles (160 km) away).^[10] Recently, new "purring" males of the same species in Hawaii are able to produce a novel auditory sexual signal that can be used to attract females while greatly reducing the likelihood of parasitoid attack from the fly.^[11]

0:00 / 0:00

The calling song of a field cricket

Flight

Some species, such as the ground crickets (Nemobiinae), are wingless; others have small fore wings and no hind wings (*Copholandrevus*), others lack hind wings and have shortened fore wings in females only, while others are macropterous, with the hind wings longer than the fore wings. In *Teleogryllus*, the proportion of macropterous individuals varies from very low to 100%. Probably, most species with hind wings longer than fore wings engage in flight.^[3]

Some species, such as *Gryllus assimilis*, take off, fly, and land efficiently and well, while other species are clumsy fliers.^[1] In some species, the hind wings are shed, leaving wing stumps, usually after dispersal of the insect by flight. In other species, they may be pulled off and consumed by the cricket itself or by another individual, probably providing a nutritional boost.^[12]

Gryllus firmus exhibits wing polymorphism; some individuals have fully functional, long hind wings and others have short wings and cannot fly. The short-winged females have smaller flight muscles, greater ovarian development, and produce more eggs, so the polymorphism adapts the cricket for either dispersal or reproduction. In some long-winged individuals, the flight muscles deteriorate during adulthood and the insect's reproductive capabilities improve.^[13]

Diet

Captive crickets are omnivorous; when deprived of their natural diet, they accept a wide range of organic foodstuffs. Some species are completely herbivorous, feeding on flowers, fruit, and leaves, with ground-based species consuming seedlings, grasses, pieces of leaf, and the shoots of young plants. Others are more predatory and include in their diet invertebrate eggs, larvae, pupae, moulting insects, scale insects, and aphids.^[14] Many are scavengers and consume various organic remains, decaying plants, seedlings, and fungi.^[15] In captivity, many species have been successfully reared on a diet of ground, commercial dry dog food, supplemented with lettuce and aphids.^[14]

Crickets have relatively powerful jaws, and several species have been known to bite humans.^[16]



Two adult domestic crickets, *Acheta domestica*, feeding on carrot

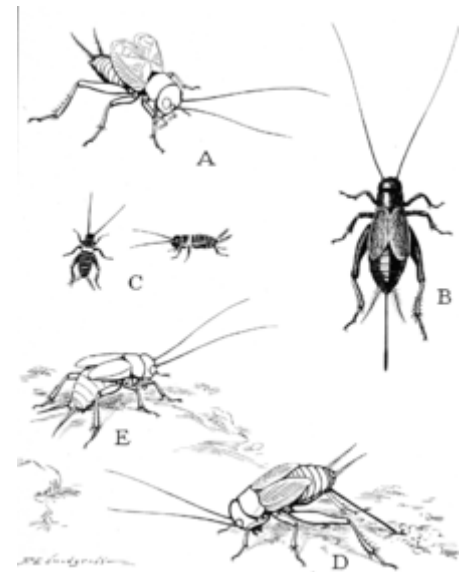
Reproduction and lifecycle

Male crickets establish their dominance over each other by aggression. They start by lashing each other with their antennae and flaring their mandibles. Unless one retreats at this stage, they resort to grappling, at the same time each emitting calls that are quite unlike those uttered in other circumstances. When one achieves dominance, it sings loudly, while the loser remains silent.^[17]

Females are generally attracted to males by their calls, though in nonstridulatory species, some other mechanism must be involved. After the pair has made antennal contact, a courtship period may occur during which the character of the call changes. The female mounts the male and a single spermatophore is transferred to the external genitalia of the female. Sperm flows from this into the female's oviduct over a period of a few minutes or up to an hour, depending on species. After copulation, the female may remove or eat the spermatophore; males may attempt to prevent this with various ritualised behaviours. The female may mate on several occasions with different males.^[18]

Most crickets lay their eggs in the soil or inside the stems of plants, and to do this, female crickets have a long, needle-like or sabre-like egg-laying organ called an ovipositor. Some ground-dwelling species have dispensed with this, either depositing their eggs in an underground chamber or pushing them into the wall of a burrow.^[1] The short-tailed cricket (*Anurogryllus*) excavates a burrow with chambers and a defecating area, lays its eggs in a pile on a chamber floor, and after the eggs have hatched, feeds the juveniles for about a month.^[19]

Crickets are hemimetabolic insects, whose lifecycle consists of an egg stage, a larval or nymph stage that increasingly resembles the adult form as the nymph grows, and an adult stage. The egg hatches into a nymph about the size of a fruit fly. This passes through about 10 larval stages, and with each successive moult, it becomes more like an adult. After the final moult, the genitalia and wings are fully developed, but a period of maturation is needed before the cricket is ready to breed.^[20]



Various instars of *Gryllus assimilis*,
by Robert Evans Snodgrass, 1930

Inbreeding avoidance

Some species of cricket are polyandrous. In *Gryllus bimaculatus*, the females select and mate with multiple viable sperm donors, preferring novel mates.^[21] Female *Teleogryllus oceanicus* crickets from natural populations similarly mate and store sperm from multiple males.^[22] Female crickets exert a postcopulatory fertilization bias in favour of unrelated males to avoid the genetic consequences of inbreeding. Fertilization bias depends on the control of sperm transport to the sperm storage organs. The inhibition of sperm storage by female crickets can act as a form of cryptic female choice to avoid the severe negative effects of inbreeding.^[23] Controlled-breeding experiments with the cricket *Gryllus firmus* demonstrated inbreeding depression, as nymphal weight and early fecundity declined substantially over the generations^[24] this was caused as expected by an increased frequency of homozygous combinations of deleterious recessive alleles.^{[24][25]}

Predators, parasites, and pathogens

Crickets have many natural enemies and are subject to various pathogens and parasites. They are eaten by large numbers of vertebrate and invertebrate predators and their hard parts are often found during the examination of animal intestines.^[4] Mediterranean house geckos (*Hemidactylus turcicus*) have learned that although a calling decorated cricket (*Gryllodes supplicans*) may be safely positioned in an out-of-reach burrow, female crickets attracted to the call can be intercepted and eaten.^[17]



Crickets are reared as food for pets and zoo animals like this baboon spider, *Pterinochilus murinus*, emerging from its den to feed.

The entomopathogenic fungus *Metarhizium anisopliae* attacks and kills crickets and has been used as the basis of control in pest populations.^[4] The insects are also affected by the cricket paralysis virus, which has caused high levels of fatalities in cricket-rearing facilities.^[26] Other fatal diseases that have been identified in mass-rearing establishments include *Rickettsia* and three further viruses. The diseases may spread more rapidly if the crickets become cannibalistic and eat the corpses.^[4]

Red parasitic mites sometimes attach themselves to the dorsal region of crickets and may greatly affect them.^[4] The horsehair worm *Paragordius varius* is an internal parasite and can control the behaviour of its cricket host and cause it to enter water, where the parasite continues its lifecycle and the cricket likely drowns.^[27] The larvae of the sarcophagid fly *Sarcophaga kellyi* develop inside the body cavity of field crickets.^[28] Female parasitic wasps of *Rhopalosoma* lay

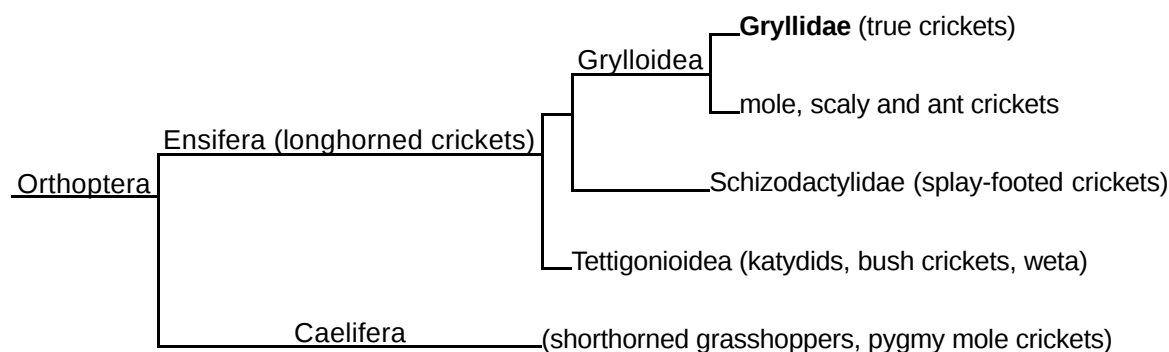
their eggs on crickets, and their developing larvae gradually devour their hosts. Other wasps in the family Scelionidae are egg parasitoids, seeking out batches of eggs laid by crickets in plant tissues in which to insert their eggs.^[4]

The fly *Ormia ochracea* has very acute hearing and targets calling male crickets. It locates its prey by ear and then lays its eggs nearby. The developing larvae burrow inside any crickets with which they come in contact and in the course of a week or so, devour what remains of the host before pupating.^[29] In Florida, the parasitic flies were only present in the autumn, and at that time of year, the males sang less but for longer periods. A trade-off exists for the male between attracting females and being parasitized.^[30]

Phylogeny and taxonomy

The phylogenetic relationships of the Gryllidae, summarized by Darryl Gwynne in 1995 from his own work (using mainly anatomical characteristics) and that of earlier authors,^[a] are shown in the following cladogram, with the Orthoptera divided into two main groups, Ensifera (crickets *sensu lato*) and Caelifera (grasshoppers). Fossil Ensifera are found from the late Carboniferous period (300 Mya) onwards,^{[31][32]} and the true crickets, Gryllidae, from the Triassic period (250 to 200 Mya).^[1]

Cladogram after Gwynne, 1995:^[31]



Fossil cricket from the Cretaceous of Brazil

A phylogenetic study by Jost & Shaw in 2006 using sequences from 18S, 28S, and 16S rRNA supported the monophyly of Ensifera. Most ensiferan families were also found to be monophyletic, and the superfamily Gryllacridoidea was found to include Stenopelmatidae, Anostostomatidae, Gryllacrididae and Lezina. Schizodactylidae and Grylloidea were shown to be sister taxa, and Rhaphidophoridae and Tettigoniidae were found to be more closely related to Grylloidea than had previously been thought. The authors stated that "a high degree of conflict exists between the molecular and morphological data, possibly indicating that much homoplasy is present in Ensifera, particularly in acoustic structures." They considered that tegmen stridulation and tibial tympanae are ancestral to Ensifera and have been lost on multiple occasions, especially within the Gryllidae.^[33]

Subfamilies

More than 900 species of Gryllidae (true crickets) are known.^{[34][b]} The family is divided into these subfamily groups, subfamilies, and extinct genera (not placed within the subfamilies):^[35]

- Subfamily group Gryllinae Laicharting, 1781 – common or field crickets
 - Gryllinae Laicharting, 1781
 - Gryllomiminae Gorochov, 1986
 - Gryllomorphinae Saussure, 1877
 - Gryllospeculinae † Gorochov, 1985
 - Itarinae Shiraki, 1930
 - Landrevinae Gorochov, 1982
 - Sclerogryllinae Gorochov, 1985
- Subfamily group Podoscirtinae
 - Euscyrtinae Gorochov, 1985
 - Hapithinae Gorochov, 1986
 - Pentacentrinae Saussure, 1878
 - Podoscirtinae Saussure, 1878 – anomalous crickets
- Subfamily group Phalangopsinae
 - Cachoplistinae Saussure, 1877
 - Paragryllinae Desutter-Grandcolas, 1987
 - Phalangopsinae Blanchard, 1845 – spider crickets
 - Phaloriinae Gorochov, 1985
 - Pteroplistinae Chopard, 1936
- Subfamily Eneopterinae Saussure, 1893 – bush crickets (American usage), not to be confused with the Tettigoniidae (katydids or bush crickets)
- Subfamily Oecanthinae Blanchard, 1845 – tree crickets
- Subfamily unplaced: extinct
 - Genus *Gryllidium* † Westwood, 1854
 - Genus *Liaonemobius* † Ren, 1998
 - Genus *Lithogryllites* † Cockerell, 1908
 - Genus *Menonia* † George, 1936
 - Genus *Nanaripegryllus* † Martins-Neto, 2002

In human culture

Folklore and myth

The folklore and mythology surrounding crickets is extensive.^[36] The singing of crickets in the folklore of Brazil and elsewhere is sometimes taken to be a sign of impending rain, or of a financial windfall. In Álvaro Núñez Cabeza de Vaca's chronicles of the Spanish conquest of the Americas, the sudden chirping of a cricket heralded the sighting of land for his crew, just as their water supply had run out.^[37] In Caraguatatuba, Brazil, a black cricket in a room is said to portend illness; a gray one, money; and a

green one, hope.^[37] In Alagoas state, northeast Brazil, a cricket announces death, thus it is killed if it chirps in a house.^[38] In Barbados, a loud cricket means money is coming in; hence, a cricket must not be killed or evicted if it chirps inside a house. However, another type of cricket that is less noisy forebodes illness or death.^[39]



Illustration for Charles Dickens's 1883 *Cricket on the Hearth* by Fred Barnard

In literature

Crickets feature as major characters in novels and children's books. Charles Dickens's 1845 novella *The Cricket on the Hearth*, divided into sections called "Chirps", tells the story of a cricket which chirps on the hearth and acts as a guardian angel to a family.^[40] Carlo Collodi's 1883 children's book "Le avventure di Pinocchio" (*The Adventures of Pinocchio*) featured "Il Grillo Parlante" (The Talking Cricket) as one of its characters.^[41] George Selden's 1960 children's book *The Cricket in Times Square* tells the story of Chester the cricket from Connecticut who joins a family and their other animals, and is taken to see Times

Square in New York.^[42] The story, which won the Newbery Honor,^[43] came to Selden on hearing a real cricket chirp in Times Square.^[44]

Souvenirs entomologiques, a book written by the French entomologist Jean-Henri Fabre, devotes a whole chapter to the cricket, discussing its construction of a burrow and its song-making. The account is mainly of the field cricket, but also mentions the Italian cricket.^[45]

Crickets have from time to time appeared in poetry. William Wordsworth's 1805 poem *The Cottager to Her Infant* includes the couplet "The kitten sleeps upon the hearth, The crickets long have ceased their mirth".^[46] John Keats's 1819 poem *Ode to Autumn* includes the lines "Hedge-crickets sing; and now with treble soft / The redbreast whistles from a garden-croft".^[47] The Chinese Tang dynasty poet Du Fu (712–770) wrote a poem that in the translation by J. P. Seaton begins "House cricket ... Trifling thing. And yet how his mournful song moves us. Out in the grass his cry was a tremble, But now, he trills beneath our bed, to share his sorrow."^[48]

As pets and fighting animals

Crickets are kept as pets and are considered good luck in some countries; in China, they are sometimes kept in cages or in hollowed-out gourds specially created in novel shapes.^[49] The practice was common in Japan for thousands of years; it peaked in the 19th century, though crickets are still sold at pet shops.^[50] It is also common to have them as caged pets in some European countries, particularly in the Iberian Peninsula. Cricket fighting is a traditional Chinese pastime that dates back to the Tang dynasty (618–907). Originally an indulgence of emperors, cricket fighting later became popular among commoners.^[51] The dominance and fighting ability of males does not depend on strength alone; it has been found that they become more aggressive after certain pre-fight



Il Grillo Parlante (The Talking Cricket) illustrated by Enrico Mazzanti for Carlo Collodi's 1883 children's book "Le avventure di Pinocchio" (*The Adventures of Pinocchio*)



Meiji period cricket holder in the form of a *norimono* palanquin, c. 1850

experiences such as isolation, or when defending a refuge. Crickets forced to fly for a short while will afterwards fight for two to three times longer than they otherwise would.^[52]

As food

In the southern part of Asia including Cambodia, Laos, Thailand, and Vietnam, crickets are commonly eaten as a snack, prepared by deep frying the soaked and cleaned insects.^[53] In Thailand, there are 20,000 farmers rearing crickets, with an estimated production of 7,500 tons per year^[54] and United Nation's FAO has implemented a project in Laos to improve cricket farming and consequently food security.^[55] The food conversion efficiency of house crickets (*Acheta domesticus*) is 1.7, some five times higher than that for beef cattle, and if their fecundity is taken into account, 15 to 20 times higher.^{[56][57]}

Cricket flour can be used as an additive to consumer foods such as pasta, bread, crackers, and cookies. The cricket flour is being used in protein bars, pet foods, livestock feed, nutraceuticals, and other industrial uses. The United Nations says the use of insect protein, such as cricket flour, could be critical in feeding the growing population of the planet while being less damaging to the environment.^[58]

Crickets are also reared as food for carnivorous zoo animals, laboratory animals, and pets.^{[4][59]} They may be "gut loaded" with additional minerals, such as calcium, to provide a balanced diet for predators such as tree frogs (Hylidae).^[60]



Deep-fried house crickets (*Acheta domesticus*) at a market in Thailand



A cricket flour energy bar with the equivalent of approximately 40 crickets in each bar.

Common expressions

By the 19th century "cricket" and "crickets" were in use as euphemisms for using Christ as an interjection. The addition of "Jiminy" (a variation of "Gemini"), sometimes shortened to "Jimmy" created the expressions "Jiminy Cricket!" or "Jimmy Crickets!" as less blasphemous alternatives to exclaiming "Jesus Christ!"^[61]

By the end of the 20th century the sound of chirping crickets came to represent quietude in literature, theatre and film. From this sentiment arose expressions equating "crickets" with silence altogether, particularly when a group of assembled people makes no noise. These expressions have grown from the more descriptive, "so quiet that you can hear crickets," to simply saying , "crickets" as shorthand for "complete silence."^[62]

In popular culture

Cricket characters feature in the Walt Disney animated movies *Pinocchio* (1940), where Jiminy Cricket becomes the title character's conscience, and in *Mulan* (1998), where Cri-kee is carried in a cage as a symbol of luck, in the Asian manner. The Crickets was the name of Buddy Holly's rock and roll band;^[63] Holly's home town baseball team in the 1990s was called the Lubbock Crickets.^[64] *Cricket* is the name of a US children's literary magazine founded in 1973; it uses a cast of insect characters.^[65] The sound of crickets is often used in media to emphasize silence, often for comic effect after an awkward joke, in a similar manner to tumbleweed.^[66]

Notes



Jiminy Cricket, from Walt Disney's movie *Pinocchio* (1940)

- a. Gwynne cites Ander 1939, Zeuner 1939, Judd 1947, Key 1970, Ragge 1977 and Rentz 1991 as supporting the two-part scheme (Ensifera, Caelifera) in his 1995 paper.^[31]
- b. Some groups in the Ensifera may be called crickets *sensu lato*, including the Rhaphidophoridae – cave or camel crickets; Stenopelmatidae – Jerusalem or sand crickets; Mogoplistidae – scaly crickets; Gryllotalpidae – mole crickets; Anabrus – mormon crickets; Myrmecophilidae – ant crickets; and Tettigoniidae – katydids or bush crickets.

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Beetle

Beetles are a group of insects that form the order **Coleoptera**, in the superorder Endopterygota. Their front pair of wings are hardened into wing-cases, elytra, distinguishing them from most other insects. The Coleoptera, with about 400,000 species, is the largest of all orders, constituting almost 40% of described insects and 25% of all known animal life-forms; new species are discovered frequently. The largest of all families, the Curculionidae (weevils), with some 83,000 member species, belongs to this order. Found in almost every habitat except the sea and the polar regions, they interact with their ecosystems in several ways: beetles often feed on plants and fungi, break down animal and plant debris, and eat other invertebrates. Some species are serious agricultural pests, such as the Colorado potato beetle, while others such as Coccinellidae (ladybirds or ladybugs) eat aphids, scale insects, thrips, and other plant-sucking insects that damage crops.

Beetles typically have a particularly hard exoskeleton including the elytra, though some such as the rove beetles have very short elytra while blister beetles have softer elytra. The general anatomy of a beetle is quite uniform and typical of insects, although there are several examples of novelty, such as adaptations in water beetles which trap air bubbles under the elytra for use while diving. Beetles are endopterygotes, which means that they undergo complete metamorphosis, with a series of conspicuous and relatively abrupt changes in body structure between hatching and becoming adult after a relatively immobile pupal stage. Some, such as stag beetles, have a marked sexual dimorphism, the males possessing enormously enlarged mandibles which they use to fight other males. Many beetles are aposematic, with bright colours and patterns warning of their toxicity, while others are harmless Batesian mimics of such insects. Many beetles, including those that live in sandy places, have effective camouflage.

Beetles are prominent in human culture, from the sacred scarabs of ancient Egypt to beetlewing art and use as pets or fighting insects for entertainment and gambling. Many beetle groups are brightly and attractively coloured making them objects of collection and decorative displays. Over 300 species are used as food, mostly as larvae; species widely consumed include mealworms and rhinoceros beetle larvae. However, the major impact of beetles on human life is as agricultural, forestry, and horticultural pests. Serious pests include the boll weevil of cotton, the Colorado potato beetle, the coconut hispine beetle, and the mountain pine beetle. Most beetles, however, do not cause economic damage and many, such as the lady beetles and dung beetles are beneficial by helping to control insect pests.

Contents

- Etymology
- Distribution and diversity
- Evolution
 - Late Paleozoic
 - Jurassic
 - Cretaceous

Beetle

Temporal range: 318–0 Ma

PreЄ

Є

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D

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PgN

Late Carboniferous–Holocene



Clockwise from top left: female golden stag beetle (*Lamprima aurata*), rhinoceros beetle (*Megasoma* sp.), long nose weevil (*Rhinotia hemistictus*), cowboy beetle (*Chondropyga dorsalis*), and a species of *Amblytelus*.

Scientific classification

Kingdom:

Animalia

Phylum:

Arthropoda

Class:

Insecta

(unranked):

Endopterygota

Order:

Coleoptera

Linnaeus, 1758

Suborders

- Adephaga
- Archostemata
- Myxophaga
- Polyphaga
- †Protocoleoptera^[1]

See subgroups of the order Coleoptera

Cenozoic

Phylogeny

External morphology

Head

Thorax

Legs

Wings

Abdomen

Anatomy and physiology

Digestive system

Nervous system

Respiratory system

Circulatory system

Specialized organs

Reproduction and development

Mating

Life cycle

Egg

Larva

Pupa and adult

Behaviour

Locomotion

Communication

Parental care

Eusociality

Feeding

Ecology

Anti-predator adaptations

Camouflage

Mimicry and aposematism

Other defences

Parasitism

Pollination

Mutualism

Tolerance of extreme environments

Migration

Relationship to humans

In ancient cultures

As pests

As beneficial resources

As food and medicine

As biodiversity indicators

In art and adornment

In entertainment

As pets

As things to collect

As inspiration for technologies

In conservation

Notes

References

Bibliography

Further reading

External links

Etymology

The name of the taxonomic order, Coleoptera, comes from the Greek *koleopteros* (κολεόπτερος), given to the group by Aristotle for their elytra, hardened shield-like forewings, from *koleos*, sheath, and *pteron*, wing. The English name beetle comes from the Old English word *bitela*, little biter, related to *bītan* (to bite),^{[2][3]} leading to Middle English *betylle*.^[4] Another Old English name for beetle is *ceafor*, chafer, used in names such as cockchafer, from the Proto-Germanic **kebrô* ("beetle"; compare German *Käfer*, Dutch *kever*).^[5]

Distribution and diversity

Beetles are by far the largest order of insects: the roughly 400,000 species make up about 40% of all insect species so far described, and about 25% of all animals.^{[1][6][7][8][9][10]} A 2015 study provided four independent estimates of the total number of beetle species, giving a mean estimate of some 1.5 million with a "surprisingly narrow range"^[11] spanning all four estimates from a minimum of 0.9 to a maximum of 2.1 million beetle species. The four estimates made use of host-specificity relationships (1.5 to 1.9 million), ratios with other taxa (0.9 to 1.2 million), plant:beetle ratios (1.2 to 1.3), and extrapolations based on body size by year of description (1.7 to 2.1 million).^{[11][12]}

Beetles are found in nearly all habitats, including freshwater and coastal habitats, wherever vegetative foliage is found, from trees and their bark to flowers, leaves, and underground near roots - even inside plants in galls, in every plant tissue, including dead or decaying ones.^[13] Tropical forest canopies have a large and diverse fauna of beetles,^[14] including Carabidae,^[15] Chrysomelidae,^[16] and Scarabaeidae.^[17]

The heaviest beetle, indeed the heaviest insect stage, is the larva of the goliath beetle, *Goliathus goliatus*, which can attain a mass of at least 115 g (4.1 oz) and a length of 11.5 cm (4.5 in). Adult male goliath beetles are the heaviest beetle in its adult stage, weighing 70–100 g (2.5–3.5 oz) and measuring up to 11 cm (4.3 in).^[18] Adult elephant beetles, *Megasoma elephas* and *Megasoma actaeon* often reach 50 g (1.8 oz) and 10 cm (3.9 in).^[19]

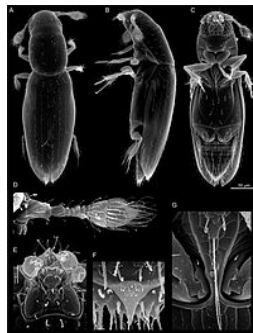
The longest beetle is the Hercules beetle *Dynastes hercules*, with a maximum overall length of at least 16.7 cm (6.6 in) including the very long pronotal horn. The smallest recorded beetle and the smallest free-living insect (as of 2015), is the featherwing beetle *Scydosella musawasensis* which may measure as little as 325 µm in length.^[20]



Coleoptera at the Staatliches Museum für Naturkunde Karlsruhe, Germany



Titan beetle, *Titanus giganteus*, a tropical longhorn, is one of the largest and heaviest insects in the world.



Scydosella musawasensis, the smallest known beetle: scale bar (right) is 50 µm.



Hercules beetle, *Dynastes hercules ecuatorianus*, the longest of all beetles

Evolution

Late Paleozoic

The oldest known fossil insect that unequivocally resembles a Coleopteran is from the Lower Permian Period about 270 million years ago (mya), though these members of the family Tshekardocoleidae have 13-segmented antennae, elytra with more fully developed venation and more irregular longitudinal ribbing, and abdomen and ovipositor extending beyond the apex of the elytra. In the Permian–Triassic extinction event at the end of the Permian, some 30% of all insect species became extinct, so the fossil record of insects only includes beetles from the Lower Triassic 220 mya. Around this time, during the Late Triassic, fungus-feeding species such as Cupedidae appear in the fossil record. In the stages of the Upper Triassic, alga-feeding insects such as Triaplidae and Hydrophilidae begin to appear, alongside predatory water beetles. The first weevils, including the Obrienidae, appear alongside the first rove beetles (Staphylinidae), which closely resemble recent species.^[21] Some entomologists are sceptical that such early insects are so closely related to present-day species, arguing that this is extremely unlikely; for example, the structure of the metepisternum suggests that the Obrienidae could be Archostemata, not weevils at all, despite fossils with weevil-like snouts.^[22]

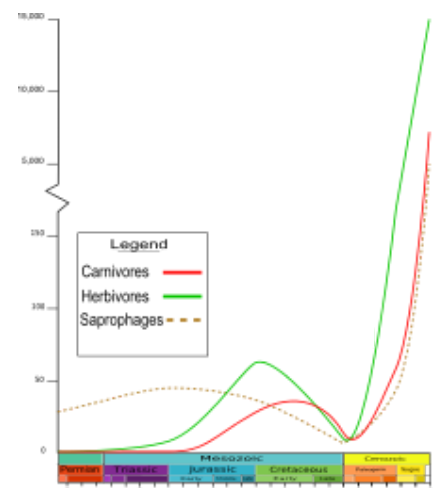
In 2009, a fossil beetle was described from the Pennsylvanian of Mazon Creek, Illinois, pushing the origin of the beetles to an earlier date, 318 to 299 mya.^[23] Fossils from this time have been found in Asia and Europe, for instance in the red slate fossil beds of Niedermoschel near Mainz, Germany.^[24] Further fossils have been found in Obora, Czech Republic and Tshekarda in the Ural mountains, Russia.^[25] However, there are only a few fossils from North America before the middle Permian, although both Asia and North America had been united to Euramerica. The first discoveries from North America made in the Wellington formation of Oklahoma were published in 2005 and 2008.^{[21][26]}

As a consequence of the Permian–Triassic extinction event, the fossil record of insects is scant, including beetles from the Lower Triassic.^[27] However, there are a few exceptions, such as in Eastern Europe. At the Babiý Kamen site in the Kuznetsk Basin, numerous beetle fossils were discovered, including entire specimens of the infraorders Archostemata (e.g. Ademosynidae, Schizocoleidae), Adephaga (e.g., Triaplidae, Trachypachidae) and Polyphaga (e.g. Hydrophilidae, Byrrhidae, Elateroidea).^[28] However, species from the families Cupedidae and Schizophoridae are not present at this site, whereas they dominate at other fossil sites from the Lower Triassic such as Khey-Yaga, Russia, in the Korotaikha Basin.^[21]

Jurassic

During the Jurassic (210 to 145 mya), there was a dramatic increase in the diversity of beetle families,^[21] including the development and growth of carnivorous and herbivorous species. The Chrysomeloidea diversified around the same time, feeding on a wide array of plant hosts from cycads and conifers to angiosperms.^[29] Close to the Upper Jurassic, the Cupedidae decreased, but the diversity of the early plant-eating species increased. Most recent plant-eating beetles feed on flowering plants or angiosperms, whose success contributed to a doubling of plant-eating species during the Middle Jurassic. However, the increase of the number of beetle families during the Cretaceous does not correlate with the increase of the number of angiosperm species.^[30] Around the same time, numerous primitive weevils (e.g. Curculionoidea) and click beetles (e.g. Elateroidea) appeared. The first jewel beetles (e.g. Buprestidae) are present, but they remained rare until the Cretaceous.^{[31][32][33]} The first scarab beetles were not coprophagous but presumably fed on rotting wood with the help of fungus; they are an early example of a mutualistic relationship.

There are more than 150 important fossil sites from the Jurassic, the majority in Eastern Europe and North Asia. Outstanding sites include Solnhofen in Upper Bavaria, Germany,^[34] Karatau in South Kazakhstan,^[35] the Yixian formation in Liaoning, North China,^[36] as well as the Jiulongshan formation and further fossil sites in Mongolia. In North America there are only a few sites with fossil records of insects from the Jurassic, namely the shell limestone deposits in the Hartford basin, the Deerfield basin and the Newark basin.^{[21][37]}



Beetle genera were mainly saprophages (detritivores) in the Permian and Triassic. During the Jurassic, herbivorous and then carnivorous genera became more common. In the Cenozoic, genera at all three trophic levels became far more numerous.

Cretaceous

The Cretaceous saw the fragmenting of the southern landmass, with the opening of the southern Atlantic Ocean and the isolation of New Zealand, while South America, Antarctica, and Australia grew more distant.^[29] The diversity of Cupedidae and Archostemata decreased considerably. Predatory ground beetles (Carabidae) and rove beetles (Staphylinidae) began to distribute into different patterns; the Carabidae predominantly occurred in the warm regions, while the Staphylinidae and click beetles (Elateridae) preferred temperate climates. Likewise, predatory species of Cleroidea and Cucujoidea hunted their prey under the bark of trees together with the jewel beetles (Buprestidae). The diversity of jewel beetles increased rapidly, as they were the primary consumers of wood,^[38] while longhorn beetles (Cerambycidae) were rather rare: their diversity increased only towards the end of the Upper Cretaceous.^[21] The first coprophagous beetles are from the Upper Cretaceous^[39] and may have lived on the excrement of herbivorous dinosaurs.^[40] The first species where both larvae and adults are adapted to an aquatic lifestyle are found. Whirligig beetles (Gyrinidae) were moderately diverse, although other early beetles (e.g. Dytiscidae) were less, with the most widespread being the species of Coptoclavidae, which preyed on aquatic fly larvae.^[21]

Many fossil sites worldwide contain beetles from the Cretaceous. Most are in Europe and Asia and belong to the temperate climate zone during the Cretaceous.^[36] Lower Cretaceous sites include the Crato fossil beds in the Araripe basin in the Ceará, North Brazil, as well as overlying Santana formation; the latter was near the equator at that time. In Spain, important sites are near Montsec and Las Hoyas. In Australia, the Koonwarra fossil beds of the Korumburra group, South Gippsland, Victoria, are noteworthy. Major sites from the Upper Cretaceous include Kzyl-Dzhar in South Kazakhstan and Arkagala in Russia.^[21]

Cenozoic

Beetle fossils are abundant in the Cenozoic; by the Quaternary (up to 1.6 mya), fossil species are identical to living ones, while from the Late Miocene (5.7 mya) the fossils are still so close to modern forms that they are most likely the ancestors of living species. The large oscillations in climate during the Quaternary caused beetles to change their geographic distributions so much that current location gives little clue to the biogeographical history of a species. It is evident that geographic isolation of populations must often have been broken as insects moved under the influence of changing climate, causing mixing of gene pools, rapid evolution, and extinctions, especially in middle latitudes.^[42]

Phylogeny

The very large number of beetle species poses special problems for classification. Some families contain tens of thousands of species, and need to be divided into subfamilies and tribes. This immense number led the evolutionary biologist J. B. S. Haldane to quip, when some theologians asked him what could be inferred about the mind of the Creator from the works of His Creation, "An inordinate fondness for beetles".^[43] Polyphaga is the largest suborder, containing more than 300,000 described species in more than 170 families, including rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), blister beetles (Meloidae), stag beetles (Lucanidae) and true weevils (Curculionidae).^{[9][44]} These polyphagan beetle groups can be identified by the presence of cervical sclerites (hardened parts of the head used as points of attachment for muscles) absent in the other suborders.^[45] Adephaga contains about 10 families of largely predatory beetles, includes ground beetles (Carabidae), water beetles (Dytiscidae) and whirligig beetles (Gyrinidae). In these insects, the testes are tubular and the first abdominal sternum (a plate of the exoskeleton) is divided by the hind coxae (the basal joints of the beetle's legs).^[46] Archostemata contains four families of mainly wood-eating beetles, including reticulated beetles (Cupedidae) and the telephone-pole beetle.^[47] The Archostemata have an exposed plate called the metatrochantin in front of the basal segment or coxa of the hind leg.^[48] Myxophaga contains about 65 described species in four families, mostly very small, including Hydroscaphidae and the genus *Sphaerius*.^[49] The myxophagan beetles are small and mostly alga-feeders. Their mouthparts are characteristic in lacking galeae and having a mobile tooth on their left mandible.^[50]

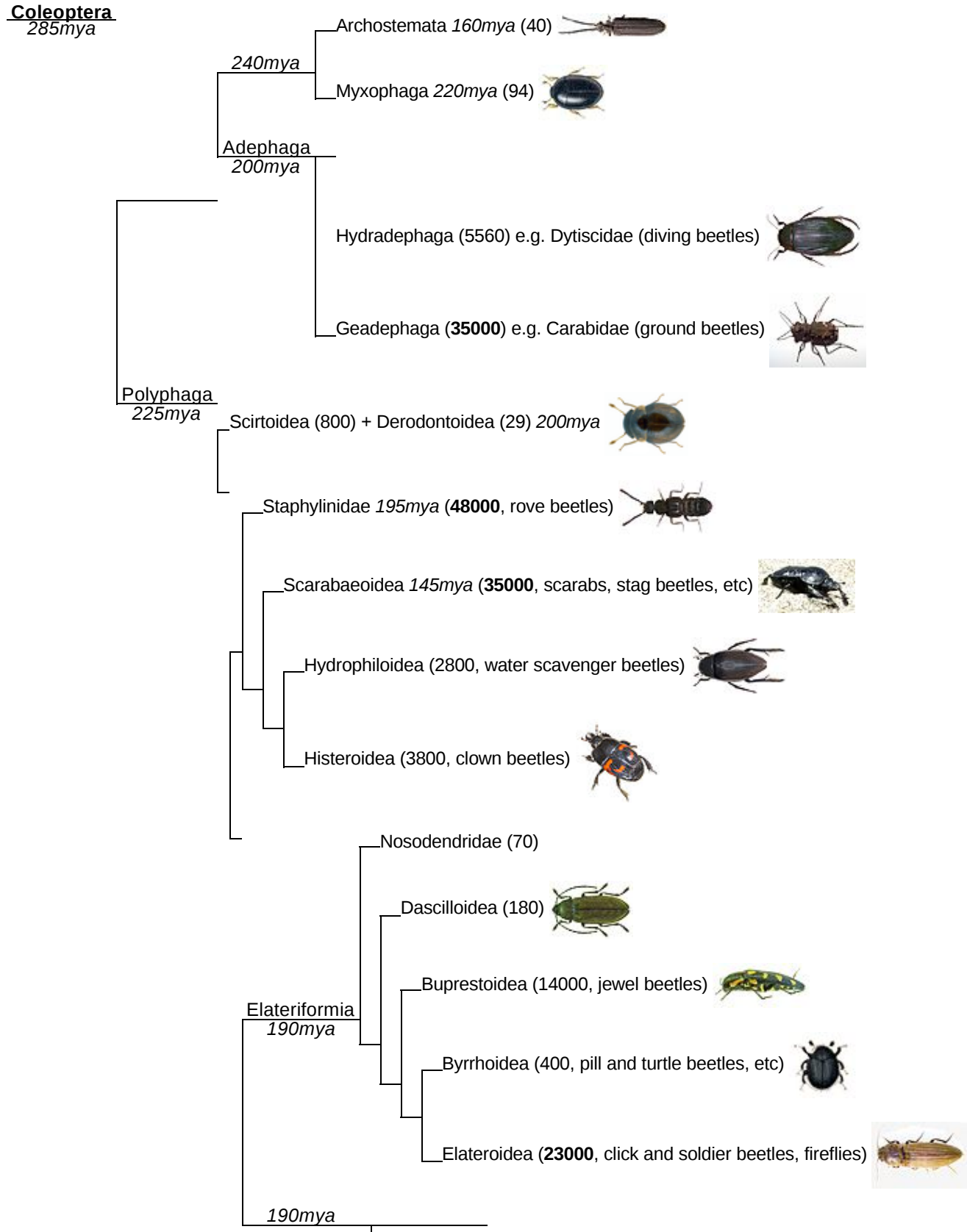
The consistency of beetle morphology, in particular their possession of elytra, has long suggested that Coleoptera is monophyletic, though there have been doubts about the arrangement of the suborders, namely the Adephaga, Archostemata, Myxophaga and Polyphaga within that clade.^{[51][29][52][53][54]} The twisted-wing parasites, Strepsiptera, are thought to be a sister group to the beetles, having split from them

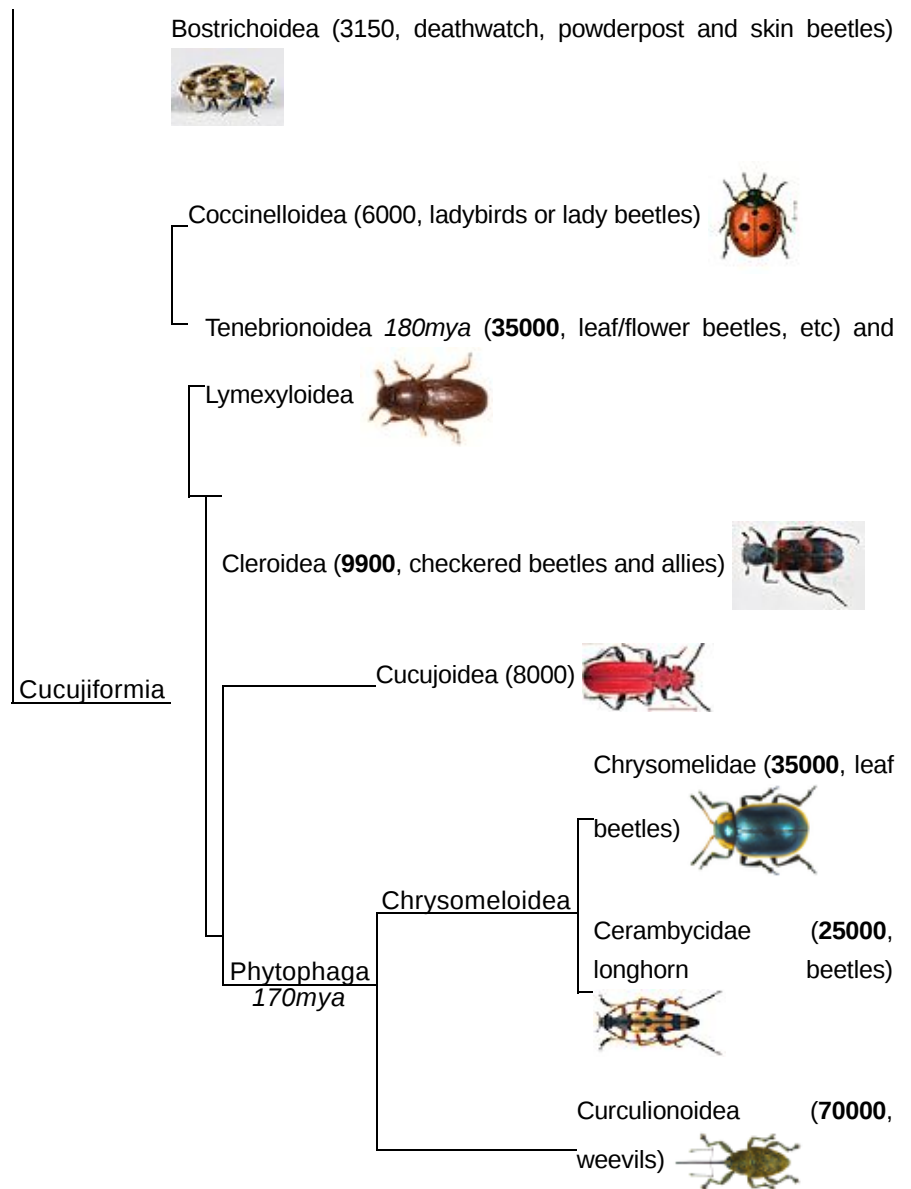


Fossil buprestid beetle from the Eocene (50 mya) Messel pit, which retains its structural color^[41]

in the Early Permian.^{[53][55][56][57]}

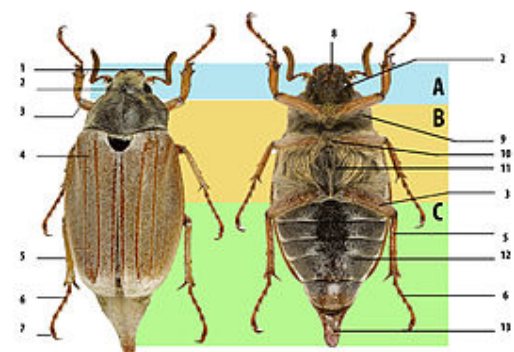
Molecular phylogenetic analysis confirms that the Coleoptera are monophyletic. Duane McKenna et al. (2015) used eight nuclear genes for 367 species from 172 of 183 Coleopteran families. They split the Adephaga into 2 clades, Hydradephaga and Geadephaga, broke up the Cucujoidea into 3 clades, and placed the Lymexyloidea within the Tenebrionoidea. The Polyphaga appear to date from the Triassic. Most extant beetle families appear to have arisen in the Cretaceous.^[57] The cladogram is based on McKenna (2015).^[57] The number of species in each group (mainly superfamilies) is shown in parentheses, and boldface if over 10,000.^[58] English common names are given where possible. Dates of origin of major groups are shown in italics in millions of years ago (mya).^[58]





External morphology

Beetles are generally characterized by a particularly hard exoskeleton and hard forewings (elytra) not usable for flying. Almost all beetles have mandibles that move in a horizontal plane. The mouthparts are rarely suctorial, though they are sometimes reduced; the maxillae always bear palps. The antennae usually have 11 or fewer segments, except in some groups like the Cerambycidae (longhorn beetles) and the Rhipiceridae (cicada parasite beetles). The coxae of the legs are usually located recessed within a coxal cavity. The genitalic structures are telescoped into the last abdominal segment in all extant beetles. Beetle larvae can often be confused with those of other endopterygote groups.^[48] The beetle's exoskeleton is made up of numerous plates, called sclerites, separated by thin sutures. This design provides armored defenses while maintaining flexibility. The general anatomy of a beetle is quite uniform, although specific organs and appendages vary greatly in appearance and function between the many families in the order. Like all insects, beetles' bodies are divided into three sections: the head, the thorax, and the abdomen.^[7] Because there are so many species, identification is quite difficult, and



Beetle body structure, using cockchafer. A: head, B: thorax, C: abdomen. 1: antenna, 2: compound eye, 3: femur, 4: elytron (wing cover), 5: tibia, 6: tarsus, 7: claws, 8: mouthparts, 9: prothorax, 10: mesothorax, 11: metathorax, 12: abdominal sternites, 13: pygidium.

relies on attributes including the shape of the antennae, the tarsal formulae^[a] and shapes of these small segments on the legs, the mouthparts, and the ventral plates (sterna, pleura, coxae). In many species accurate identification can only be made by examination of the unique male genitalic structures.^[59]

Head

The head, having mouthparts projecting forward or sometimes downturned, is usually heavily sclerotized and is sometimes very large.^[6] The eyes are compound and may display remarkable adaptability, as in the case of the aquatic whirligig beetles (Gyrinidae), where they are split to allow a view both above and below the waterline. A few Longhorn beetles (Cerambycidae) and weevils as well as some fireflies (Rhagophthalmidae)^[60] have divided eyes, while many have eyes that are notched, and a few have ocelli, small, simple eyes usually farther back on the head (on the vertex); these are more common in larvae than in adults.^[61] The anatomical organization of the compound eyes may be modified and depends on whether a species is primarily crepuscular, or diurnally or nocturnally active.^[62] Ocelli are found in the adult carpet beetle (Dermestidae), some rove beetles (Omaliinae), and the Derodontidae.^[61]



Polyphylla fullo has distinctive fan-like antennae, one of several distinct forms for the appendages among beetles.

Beetle antennae are primarily organs of sensory perception and can detect motion, odour and chemical substances,^[63] but may also be used to physically feel a beetle's environment. Beetle families may use antennae in different ways. For example, when moving quickly, tiger beetles may not be able to see very well and instead hold their antennae rigidly in front of them in order to avoid obstacles.^[64] Certain Cerambycidae use antennae to balance, and blister beetles may use them for grasping. Some aquatic beetle species may use antennae for gathering air and passing it under the body whilst submerged. Equally, some families use antennae during mating, and a few species use them for defence. In the cerambycid *Onychocerus albitarsis*, the antennae have venom injecting structures used in defence, which is unique among arthropods.^[65] Antennae vary greatly in form, sometimes between the sexes, but are often similar within any given family. Antennae may be clubbed, threadlike, angled, shaped like a string of beads, comb-like (either on one side or both, bipectinate), or toothed. The physical variation of antennae is important for the identification of many beetle groups. The Curculionidae have elbowed or geniculate antennae. Feather like flabellate antennae are a restricted

form found in the Rhipiceridae and a few other families. The Silphidae have a capitate antennae with a spherical head at the tip. The Scarabaeidae typically have lamellate antennae with the terminal segments extended into long flat structures stacked together. The Carabidae typically have thread-like antennae. The antennae arises between the eye and the mandibles and in the Tenebrionidae, the antennae rise in front of a notch that breaks the usually circular outline of the compound eye. They are segmented and usually consist of 11 parts, the first part is called the scape and the second part is the pedicel. The other segments are jointly called the flagellum.^{[63][66][67]}

Beetles have mouthparts like those of grasshoppers. The mandibles appear as large pincers on the front of some beetles. The mandibles are a pair of hard, often tooth-like structures that move horizontally to grasp, crush, or cut food or enemies (see defence, below). Two pairs of finger-like appendages, the maxillary and labial palpi, are found around the mouth in most beetles, serving to move food into the mouth. In many species, the mandibles are sexually dimorphic, with those of the males enlarged enormously compared with those of females of the same species.^[6]

Thorax

The thorax is segmented into the two discernible parts, the pro- and pterothorax. The pterothorax is the fused meso- and metathorax, which are commonly separated in other insect species, although flexibly articulate from the prothorax. When viewed from below, the thorax is that part from which all three pairs of legs and both pairs of wings arise. The abdomen is everything posterior to the thorax.^[7] When viewed from above, most beetles appear to have three clear sections, but this is deceptive: on the beetle's upper surface, the middle section is a hard plate called the pronotum, which is only the front part of the thorax; the back part of the thorax is concealed by the beetle's wings. This further segmentation is usually best seen on the abdomen.^[68]

Legs

The multisegmented legs end in two to five small segments called tarsi. Like many other insect orders, beetles have claws, usually one pair, on the end of the last tarsal segment of each leg. While most beetles use their legs for walking, legs have been variously adapted for other uses. Aquatic beetles including the Dytiscidae (diving beetles), Haliplidae, and many species of Hydrophilidae, the legs, often the last pair, are modified for swimming, typically with rows of long hairs. Male diving beetles have suctional cups on their forelegs that they use to grasp females.^[69] Other beetles have fossorial legs widened and often spined for digging. Species with such adaptations are found among the scarabs, ground beetles, and clown beetles (Histeridae). The hind legs of some beetles, such as flea beetles (within Chrysomelidae) and flea weevils (within Curculionidae), have enlarged femurs that help them leap.^[70]



Acilius sulcatus, a diving beetle with hind legs adapted as swimming limbs

Wings



Checkered beetle *Trichodes alvearius* taking off, showing the hard elytra (forewings adapted as wing-cases) held stiffly away from the flight wings

The forewings of beetles are not used for flight, but form elytra which cover the hind part of the body and protect the hindwings. The elytra are usually hard shell-like structures which must be raised to allow the hind wings to move for flight.^[71] However, in the soldier beetles (Cantharidae), the elytra are soft, earning this family the name of leatherwings.^[72] Other soft wing beetles include the net-winged beetle *Calopteron discrepans*, which has brittle wings that rupture easily in order to release chemicals for defence.^[73]

Beetles' flight wings are crossed with veins and are folded after landing, often along these veins, and stored below the elytra. A fold (*jugum*) of the membrane at the base of each wing is characteristic.^[71] Some beetles have lost the ability to fly. These include some ground beetles (Carabidae) and some true weevils (Curculionidae), as well as desert- and cave-dwelling species of other families. Many have the two elytra fused together, forming a solid shield over the abdomen. In a few families, both the ability to fly and the elytra have been lost, as in the glow-worms (Phengodidae), where the females resemble larvae throughout their lives.^[74] The presence of elytra and wings does not always indicate that the beetle will fly. For example, the tansy beetle walks between habitats despite being physically capable of flight.^[75]

Abdomen

The abdomen is the section behind the metathorax, made up of a series of rings, each with a hole for breathing and respiration, called a spiracle, composing three different segmented sclerites: the tergum, pleura, and the sternum. The tergum in almost all species is membranous, or usually soft and concealed by the wings and elytra when not in flight. The pleura are usually small or hidden in some species, with each pleuron having a single spiracle. The sternum is the most widely visible part of the abdomen, being a more or less sclerotized segment. The abdomen itself does not have any appendages, but some (for example, Mordellidae) have articulating sternal lobes.^[76]

Anatomy and physiology

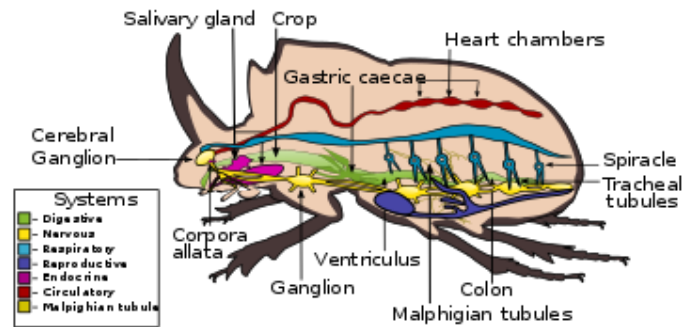
Digestive system

The digestive system of beetles is primarily adapted for a herbivorous diet. Digestion takes place mostly in the anterior midgut, although in predatory groups like the Carabidae, most digestion occurs in the crop by means of midgut enzymes. In the Elateridae, the larvae are liquid feeders that extraorally digest their food by secreting enzymes.^[7] The alimentary canal basically consists of a short, narrow pharynx, a widened expansion, the crop, and a poorly developed gizzard. This is followed by the midgut, that varies in dimensions

between species, with a large amount of cecum, and the hindgut, with varying lengths. There are typically four to six Malpighian tubules.^[6]

Nervous system

The nervous system in beetles contains all the types found in insects, varying between different species, from three thoracic and seven or eight abdominal ganglia which can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure.^[7]



A beetle's body systems

Respiratory system



Dytiscus spiracles (right) on upper side of abdomen, normally covered by the elytra, are in contact with an air bubble when the beetle dives.

Like most insects, beetles inhale air, for the oxygen it contains, and exhale carbon dioxide, via a tracheal system. Air enters the body through spiracles, and circulates within the haemocoel in a system of tracheae and tracheoles, through whose walls the gases can diffuse.^[7]

Diving beetles, such as the Dytiscidae, carry a bubble of air with them when they dive. Such a bubble may be contained under the elytra or against the body by specialized hydrophobic hairs. The bubble covers at least some of the spiracles, permitting air to enter the tracheae.^[7] The function of the bubble is not only to contain a store of air but to act as a physical gill. The air that it traps is in contact with oxygenated water, so as the animal's consumption depletes the oxygen in the bubble, more oxygen can diffuse in to replenish it.^[77] Carbon dioxide is more soluble in water than either oxygen or nitrogen, so it readily diffuses out faster than in. Nitrogen is the most plentiful gas in the bubble, and the least soluble, so it constitutes a relatively static component of the bubble and acts as a stable medium for respiratory gases to accumulate in and pass through. Occasional visits to the surface are sufficient for the beetle to re-establish the constitution of the bubble.^[78]

Circulatory system

Like other insects, beetles have open circulatory systems, based on hemolymph rather than blood. As in other insects, a segmented tube-like heart is attached to the dorsal wall of the hemocoel. It has paired inlets or *ostia* at intervals down its length, and circulates the hemolymph from the main cavity of the haemocoel and out through the anterior cavity in the head.^[79]

Specialized organs

Different glands are specialized for different pheromones to attract mates. Pheromones from species of Rutelinae are produced from epithelial cells lining the inner surface of the apical abdominal segments; amino acid-based pheromones of Melolonthinae are produced from eversible glands on the abdominal apex. Other species produce different types of pheromones. Dermestids produce esters, and species of Elateridae produce fatty acid-derived aldehydes and acetates.^[7] To attract a mate, fireflies (Lampyridae) use modified fat body cells with transparent surfaces backed with reflective uric acid crystals to produce light by bioluminescence. Light production is highly efficient, by oxidation of luciferin catalyzed by enzymes (luciferases) in the presence of adenosine triphosphate (ATP) and oxygen, producing oxyluciferin, carbon dioxide, and light.^[7]

Tympanal organs or hearing organs consist of a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons, are found in two families.^[80] Several species of the genus *Cicindela* (Carabidae) have hearing organs on the dorsal surfaces of their first abdominal segments beneath the wings; two tribes in the Dynastinae (within the Scarabaeidae) have hearing organs just beneath their pronotal shields or neck membranes. Both families are sensitive to ultrasonic frequencies, with strong evidence indicating they function to detect the presence of bats by their ultrasonic echolocation.^[7]

Reproduction and development

Beetles are members of the superorder Endopterygota, and accordingly most of them undergo complete metamorphosis. The typical form of metamorphosis in beetles passes through four main stages: the egg, the larva, the pupa, and the imago or adult. The larvae are commonly called grubs and the pupa sometimes is called the chrysalis. In some species, the pupa may be enclosed in a cocoon constructed by the larva towards the end of its final instar. Some beetles, such as typical members of the families Meloidae and Rhipiphoridae, go further, undergoing hypermetamorphosis in which the first instar takes the form of a triungulin.^[81]

Mating

Some beetles have intricate mating behaviour. Pheromone communication is often important in locating a mate. Different species use different pheromones. Scarab beetles such as the Rutelinae use pheromones derived from fatty acid synthesis, while other scarabs such as the Melolonthinae use amino acids and terpenoids. Another way beetles find mates is seen in the fireflies (Lampyridae) which are bioluminescent, with abdominal light-producing organs. The males and females engage in a complex dialogue before mating; each species has a unique combination of flight patterns, duration, composition, and intensity of the light produced.^[7]

Before mating, males and females may stridulate, or vibrate the objects they are on. In the Meloidae, the male climbs onto the dorsum of the female and strokes his antennae on her head, palps, and antennae. In *Eupompha*, the male draws his antennae along his longitudinal vertex. They may not mate at all if they do not perform the precopulatory ritual.^[7] This mating behaviour may be different amongst dispersed populations of the same species. For example, the mating of a Russian population of tansy beetle (*Chysolina graminis*) is preceded by an elaborate ritual involving the male tapping the female's eyes, pronotum and antennae with its antennae, which is not evident in the population of this species in the United Kingdom.^[82]

Competition can play a part in the mating rituals of species such as burying beetles (*Nicrophorus*), the insects fighting to determine which can mate. Many male beetles are territorial and fiercely defend their territories from intruding males. In such species, the male often has horns on the head or thorax, making its body length greater than that of a female. Copulation is generally quick, but in some cases lasts for several hours. During copulation, sperm cells are transferred to the female to fertilize the egg.^[6]

Life cycle

Egg

Essentially all beetles lay eggs, though some myrmecophilous Aleocharinae and some Chrysomelinae which live in mountains or the subarctic are ovoviviparous, laying eggs which hatch almost immediately. Beetle eggs generally have smooth surfaces and are soft, though the Cupedidae have hard eggs. Eggs vary widely between species: the eggs tend to be small in species with many instars (larval stages), and in those that lay large numbers of eggs. A female may lay from several dozen to several thousand eggs during her lifetime, depending on the extent of parental care. This ranges from the simple laying of eggs under a leaf, to the parental care provided by scarab beetles, which house, feed and protect their young. The Attelabidae roll leaves and lay their eggs inside the roll for protection.^{[7][83]}

Larva

The larva is usually the principal feeding stage of the beetle life cycle. Larvae tend to feed voraciously once they emerge from their eggs. Some feed externally on plants, such as those of certain leaf beetles, while others feed within their food sources. Examples of internal feeders are most Buprestidae and longhorn beetles. The larvae of many beetle families are predatory like the adults (ground beetles, ladybirds, rove beetles). The larval period varies between species, but can be as long as several years. The larvae of skin beetles undergo a degree of reversed development when starved, and later grow back to the previously attained level of maturity. The cycle can be repeated



Punctate flower chafers (*Neorrhina punctata*, Scarabaeidae) mating

many times (see Biological immortality).^[84] Larval morphology is highly varied amongst species, with well-developed and sclerotized heads, distinguishable thoracic and abdominal segments (usually the tenth, though sometimes the eighth or ninth).^[6]



Scarabaeiform larva of Hercules beetle

Beetle larvae can be differentiated from other insect larvae by their hardened, often darkened heads, the presence of chewing mouthparts, and spiracles along the sides of their bodies. Like adult beetles, the larvae are varied in appearance, particularly between beetle families. Beetles with somewhat flattened, highly mobile larvae include the ground beetles and rove beetles; their larvae are described as campodeiform. Some beetle larvae resemble hardened worms with dark head capsules and minute legs. These are elateriform larvae, and are found in the

click beetle (Elateridae) and darkling beetle (Tenebrionidae) families. Some elateriform larvae of click beetles are known as wireworms. Beetles in the Scarabaeoidea have short, thick larvae described as scarabaeiform, more commonly known as grubs.^[85]

All beetle larvae go through several instars, which are the developmental stages between each moult. In many species, the larvae simply increase in size with each successive instar as more food is consumed. In some cases, however, more dramatic changes occur. Among certain beetle families or genera, particularly those that exhibit parasitic lifestyles, the first instar (the planidium) is highly mobile to search out a host, while the following instars are more sedentary and remain on or within their host. This is known as hypermetamorphosis; it occurs in the Meloidae, Micromalthidae, and Ripiphoridae.^[86] The blister beetle *Epicauta vittata* (Meloidae), for example, has three distinct larval stages. Its first stage, the triungulin, has longer legs to go in search of the eggs of grasshoppers. After feeding for a week it moults to the second stage, called the caraboid stage, which resembles the larva of a carabid beetle. In another week it moults and assumes the appearance of a scarabaeid larva – the scarabaeidoid stage. Its penultimate larval stage is the pseudo-pupa or the coarctate larva, which will overwinter and pupate until the next spring.^[87]

The larval period can vary widely. A fungus feeding staphylinid *Phanerota fasciata* undergoes three moults in 3.2 days at room temperature while *Anisotoma* sp. (Leioididae) completes its larval stage in the fruiting body of slime mold in 2 days and possibly represents the fastest growing beetles. Dermestid beetles, *Trogoderma inclusum* can remain in an extended larval state under unfavourable conditions, even reducing their size between moults. A larva is reported to have survived for 3.5 years in an enclosed container.^[7]

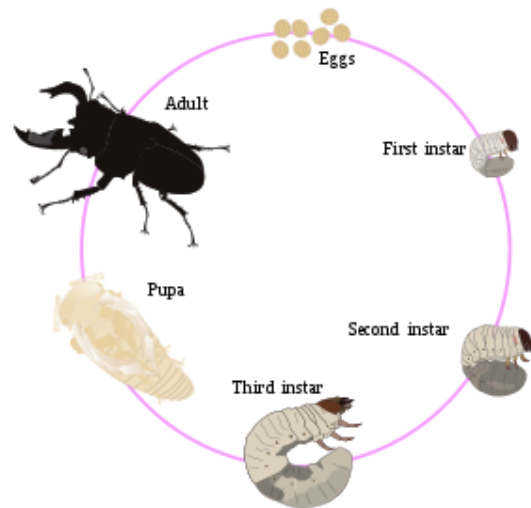
Pupa and adult

As with all endopterygotes, beetle larvae pupate, and from these pupae emerge fully formed, sexually mature adult beetles, or imagos. Pupae never have mandibles (they are adecticous). In most pupae, the appendages are not attached to the body and are said to be exarate; in a few beetles (Staphylinidae, Ptiliidae etc.) the appendages are fused with the body (termed as obtect pupae).^[6]

Adults have extremely variable lifespans, from weeks to years, depending on the species.^{[6][48]} Some wood-boring beetles can have extremely long life-cycles. It is believed that when furniture or house timbers are infested by beetle larvae, the timber already contained the larvae when it was first sawn up. A birch bookcase 40 years old released adult *Eburia quadrigeminata* (Cerambycidae), while *Buprestis aurulenta* and other Buprestidae have been documented as emerging as much as 51 years after manufacture of wooden items.^[88]

Behaviour

Stag Beetle Life Cycle



The life cycle of the stag beetle includes three instars.

Locomotion



Photinus pyralis, firefly, in flight

The elytra allow beetles to both fly and move through confined spaces, doing so by folding the delicate wings under the elytra while not flying, and folding their wings out just before takeoff. The unfolding and folding of the wings is operated by muscles attached to the wing base; as long as the tension on the radial and cubital veins remains, the wings remain straight. In some day-flying species (for example, Buprestidae, Scarabaeidae), flight does not include large amounts of lifting of the elytra, having the metathorac wings extended



The ivory-marked beetle, *Eburia quadrigeminata*, may live up to 40 years inside the hardwoods on which the larva feeds.

under the lateral elytra margins.^[7] The altitude reached by beetles in flight varies. One study investigating the flight altitude of the ladybird species *Coccinella septempunctata* and *Harmonia axyridis* using radar showed that, whilst the majority in flight over a single location were at 150–195 m above ground level, some reached altitudes of over 1100 m.^[89]

Many rove beetles have greatly reduced elytra, and while they are capable of flight, they most often move on the ground: their soft bodies and strong abdominal muscles make them flexible, easily able to wriggle into small cracks.^[90]

Aquatic beetles use several techniques for retaining air beneath the water's surface. Diving beetles (Dytiscidae) hold air between the abdomen and the elytra when diving. Hydrophilidae have hairs on their under surface that retain a layer of air against their bodies. Adult crawling water beetles use both their elytra and their hind coxae (the basal segment of the back legs) in air retention, while whirligig beetles simply carry an air bubble down with them whenever they dive.^[91]

Communication

Beetles have a variety of ways to communicate, including the use of pheromones. The mountain pine beetle emits a pheromone to attract other beetles to a tree. The mass of beetles are able to overcome the chemical defenses of the tree. After the tree's defenses have been exhausted, the beetles emit an anti-aggregation pheromone. This species can stridulate to communicate,^[92] but others may use sound to defend themselves when attacked.^[93]

Parental care

Parental care is found in a few families^[94] of beetle, perhaps for protection against adverse conditions and predators.^[7] The rove beetle *Bledius spectabilis* lives in salt marshes, so the eggs and larvae are endangered by the rising tide. The maternal beetle patrols the eggs and larvae, burrowing to keep them from flooding and asphyxiating, and protects them from the predatory carabid beetle *Dicheirotichus gustavi* and from the parasitoidal wasp *Barycnemis blediator*, which kills some 15% of the larvae.^[95]

Burying beetles are attentive parents, and participate in cooperative care and feeding of their offspring. Both parents work to bury small animal carcass to serve as a food resource for their young and build a brood chamber around it. The parents prepare the carcass and protect it from competitors and from early decomposition. After their eggs hatch, the parents keep the larvae clean of fungus and bacteria and help the larvae feed by regurgitating food for them.^[96]

Some dung beetles provide parental care, collecting herbivore dung and laying eggs within that food supply, an instance of mass provisioning. Some species do not leave after this stage, but remain to safeguard their offspring.^[97]



A dung beetle rolling dung

Most species of beetles do not display parental care behaviors after the eggs have been laid.^[98]

Subsociality, where females guard their offspring, is well-documented in two families of Chrysomelidae, Cassidinae and Chrysomelinae.^{[99][100][101][102][103]}

Eusociality

Eusociality involves cooperative brood care (including brood care of offspring from other individuals), overlapping generations within a colony of adults, and a division of labour into reproductive and non-reproductive groups.^[104] Few organisms outside Hymenoptera exhibit this behavior; the only beetle to do so is the weevil *Austroplatypus incompertus*.^[105] This Australian species lives in horizontal networks of tunnels, in the heartwood of *Eucalyptus* trees. It is one of more than 300 species of wood-boring Ambrosia beetles which distribute the spores of ambrosia fungi.^[106] The fungi grow in the beetles' tunnels, providing food for the beetles and their larvae; female offspring remain in the tunnels and maintain the fungal growth, probably never reproducing.^{[106][105]} Cooperative brood care is also found in the bess beetles (Passalidae) where the larvae feed on the semi-digested faeces of the adults.^[107]

Feeding



Hycleus sp. (Meloidae) feeding on the petals of *Ipomoea carnea*

Beetles are able to exploit a wide diversity of food sources available in their many habitats. Some are omnivores, eating both plants and animals. Other beetles are highly specialized in their diet. Many species of leaf beetles, longhorn beetles, and weevils are very host-specific, feeding on only a single species of plant. Ground beetles and rove beetles (Staphylinidae), among others, are primarily carnivorous and catch and consume many other arthropods and small prey, such as earthworms and snails. While most predatory beetles are generalists, a few species have more specific prey requirements or preferences.^[108]

Decaying organic matter is a primary diet for many species. This can range from dung, which is consumed by coprophagous species (such as certain scarab beetles in the Scarabaeidae), to dead animals, which are eaten by necrophagous species (such as the carrion beetles, Silphidae). Some beetles found in dung and carrion are in fact predatory. These include members of the Histeridae and Silphidae, preying on the larvae of coprophagous and necrophagous insects.^[109] Many beetles feed under bark, some feed on wood while others feed on fungi growing on wood or leaf-litter. Some beetles have special mycangia, structures for the transport of fungal spores.^[110]

Ecology

Anti-predator adaptations

Beetles, both adults and larvae, are the prey of many animal predators including mammals from bats to rodents, birds, lizards, amphibians, fishes, dragonflies, robberflies, reduviid bugs, ants, other beetles, and spiders.^{[111][112]} Beetles use a variety of anti-predator adaptations to defend themselves. These include camouflage and mimicry against predators that hunt by sight, toxicity, and defensive behaviour.

Camouflage

Camouflage is common and widespread among beetle families, especially those that feed on wood or vegetation, such as leaf beetles (Chrysomelidae, which are often green) and weevils. In some species, sculpturing or various coloured scales or hairs cause beetles such as the avocado weevil *Heilipus apiatus* to resemble bird dung or other inedible objects.^[111] Many beetles that live in sandy environments blend in with the coloration of that substrate.^[113]



A camouflaged longhorn beetle, *Ecyrus dasycerus*

Mimicry and aposematism



Clytus arietis (Cerambycidae), a Batesian mimic of wasps



The bloody-nosed beetle, *Timarcha tenebricosa*, defending itself by releasing a droplet of noxious red liquid (base of leg, on right)

Some longhorn beetles (Cerambycidae) are effective Batesian mimics of wasps. Beetles may combine coloration with behavioural mimicry, acting like the wasps they already closely resemble. Many other beetles, including ladybirds, blister beetles, and lycid beetles secrete distasteful or toxic substances to make them unpalatable or poisonous, and are often aposematic, where bright or contrasting coloration warn off predators; many beetles and other insects mimic these chemically protected species.^[114]

Chemical defense is important in some species, usually being advertised by bright aposematic colours. Some Tenebrionidae use their posture for releasing noxious chemicals to warn off predators. Chemical defences may serve

purposes other than just protection from vertebrates, such as protection from a wide range of microbes. Some species sequester chemicals from the plants they feed on, incorporating them into their own defenses.^[113]

Other species have special glands to produce deterrent chemicals. The defensive glands of carabid ground beetles produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. African carabid beetles (for example, *Anthia* and *Thermophilum* – *Thermophilum* is sometimes included within *Anthia*) employ the same chemicals as ants: formic acid.^[114] Bombardier beetles have well-developed pygidial glands that empty from the sides of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers, one for hydroquinones and hydrogen peroxide, the other holding hydrogen peroxide and catalase enzymes. These chemicals mix and result in an explosive ejection, reaching a temperature of around 100 °C (212 °F), with the breakdown of hydroquinone to hydrogen, oxygen, and quinone. The oxygen propels the noxious chemical spray as a jet that can be aimed accurately at predators.^[7]



Blister beetles such as *Hycleus* have brilliant aposematic coloration, warning of their toxicity.

Other defences

Large ground-dwelling beetles such as Carabidae, the rhinoceros beetle and the longhorn beetles defend themselves using strong mandibles, or heavily sclerotised (armored) spines or horns to deter or fight off predators.^[113] Many species of weevil that feed out in the open on leaves of plants react to attack by employing a drop-off reflex. Some combine it with thanatosis, in which they close up their appendages and "play dead".^[115] The click beetles (Elateridae) can suddenly catapult themselves out of danger by releasing the energy stored by a click mechanism, which consists of a stout spine on the prosternum and a matching groove in the mesosternum.^[111] Some species startle an attacker by producing sounds through a process known as stridulation.^[93]

Parasitism

A few species of beetles are ectoparasitic on mammals. One such species, *Platypyllus castoris*, parasitises beavers (*Castor* spp.). This beetle lives as a parasite both as a larva and as an adult, feeding on epidermal tissue and possibly on skin secretions and wound exudates. They are strikingly flattened dorsoventrally, no doubt as an adaptation for slipping between the beavers' hairs. They are wingless and eyeless, as are many other ectoparasites.^[116] Others are kleptoparasites of other invertebrates, such as the small hive beetle (*Aethina tumida*) that infests honey bee nests,^[117] while many species are parasitic inquiline or commensal in the nests of ants.^[118] A few groups of beetles are primary parasitoids of other insects, feeding off of, and eventually killing their hosts.^[119]

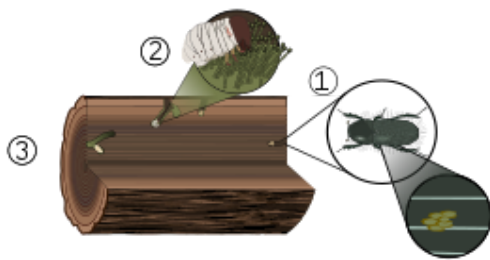
Pollination

Beetle-pollinated flowers are usually large, greenish or off-white in color, and heavily scented. Scents may be spicy, fruity, or similar to decaying organic material. Beetles were most likely the first insects to pollinate flowers. Most beetle-pollinated flowers are flattened or dish-shaped, with pollen easily accessible, although they may include traps to keep the beetle longer. The plants' ovaries are usually well protected from the biting mouthparts of their pollinators. The beetle families that habitually pollinate flowers are the Buprestidae, Cantharidae, Cerambycidae, Cleridae, Dermestidae, Lycidae, Melyridae, Mordellidae, Nitidulidae and Scarabaeidae.^[120] Beetles may be particularly important in some parts of the world such as semiarid areas of southern Africa and southern California^[121] and the montane grasslands of KwaZulu-Natal in South Africa.^[122]



An Israeli Copper Flower-Chafer (*Protaetia cuprea ignicollis*) pollinating a crown daisy (*Glebionis coronaria*)

Mutualism



- 1: Adult ambrosia beetle burrows into wood and lays eggs, carrying fungal spores in its mycangia.
- 2: Larva feeds on fungus, which digests wood, removing toxins, to mutual benefit.
- 3: Larva pupates.

Mutualism is well known in a few beetles, such as the ambrosia beetle, which partners with fungi to digest the wood of dead trees.

The beetles excavate tunnels in dead trees in which they cultivate fungal gardens, their sole source of nutrition. After landing on a suitable tree, an ambrosia beetle excavates a tunnel in which it releases spores of its fungal symbiont. The fungus penetrates the plant's xylem tissue, digests it, and concentrates the nutrients on and near the surface of the beetle gallery, so the weevils and the fungus both benefit. The beetles cannot eat the wood due to toxins, and uses its relationship with fungi to help overcome the defenses of its host tree in order to provide nutrition for their larvae.^[123] Chemically mediated by a bacterially produced polyunsaturated peroxide,^[124] this mutualistic relationship between the beetle and the fungus is coevolved.^{[123][125]}

Tolerance of extreme environments

About 90% of beetle species enter a period of adult diapause, a quiet phase with reduced metabolism to tide unfavourable environmental conditions. Adult diapause is the most common form of diapause in Coleoptera. To endure the period without food (often lasting many months) adults prepare by accumulating reserves of lipids, glycogen, proteins and other substances needed for resistance to future hazardous changes of environmental conditions. This diapause is induced by signals heralding the arrival of the unfavourable season; usually the cue is photoperiodic. Short (decreasing) day length serves as a signal of approaching winter and induces winter diapause (hibernation).^[126] A study of hibernation in the Arctic beetle *Pterostichus brevicornis* showed that the body fat levels of adults were highest in autumn with the alimentary canal filled with food, but empty by the end of January. This loss of body fat was a gradual process, occurring in combination with dehydration.^[127]



Beetle found in Thar Desert

All insects are poikilothermic,^[128] so the ability of a few beetles to live in extreme environments depends on their resilience to unusually high or low temperatures. The bark beetle *Pityogenes chalcographus* can survive -39°C whilst overwintering beneath tree bark,^[129] the Alaskan beetle *Cucujus clavipes puniceus* is able to withstand -58°C ; its larvae may survive -100°C .^[130] At these low temperatures, the formation of ice crystals in internal fluids is the biggest threat to survival to beetles, but this is prevented through the production of antifreeze proteins that stop water molecules from grouping together. The low temperatures experienced by *Cucujus clavipes* can be survived through their deliberate dehydration in conjunction with the antifreeze proteins. This concentrates the antifreezes several fold.^[131] The hemolymph of the mealworm beetle *Tenebrio molitor* contains several antifreeze proteins.^[132] The Alaskan beetle *Upis ceramoides* can survive -60°C : its cryoprotectants are xylomannan, a molecule consisting of a sugar bound to a fatty acid,^[133] and the sugar-alcohol, threitol.^[134]

Conversely, desert dwelling beetles are adapted to tolerate high temperatures. For example, the Tenebrionid beetle *Onymacris rugatipennis* can withstand 50 °C.^[135] Tiger beetles in hot, sandy areas are often whitish (for example, *Habroscelimorpha dorsalis*), to reflect more heat than a darker colour would. These beetles also exhibits behavioural adaptations to tolerate the heat: they are able to stand erect on their tarsi to hold their bodies away from the hot ground, seek shade, and turn to face the sun so that only the front parts of their heads are directly exposed.^[136]



The fogstand beetle of the Namib Desert, *Stenocara gracilipes* is able to survive by collecting water from fog on its back.

The fogstand beetle of the Namib Desert, *Stenocara gracilipes*, is able to collect water from fog, as its elytra have a textured surface combining hydrophilic (water-loving) bumps and waxy, hydrophobic troughs. The beetle faces the early morning breeze, holding up its abdomen; droplets condense on the elytra and run along ridges towards their mouthparts. Similar adaptations are found in several other Namib desert beetles such as *Onymacris unguicularis*.^[137]

Some terrestrial beetles that exploit shoreline and floodplain habitats have physiological adaptations for surviving floods. In the event of flooding, adult beetles may be mobile enough to move away from flooding, but larvae and pupa often cannot. Adults of *Cicindela togata* are unable to survive immersion in water, but larvae are able to survive a prolonged period, up to 6 days, of anoxia during floods. Anoxia tolerance in the larvae may have been sustained by switching to anaerobic metabolic pathways or by reducing metabolic rate.^[138] Anoxia tolerance in the adult Carabid beetle *Pelophilus borealis* was tested in laboratory conditions and it was found that they could survive a continuous period of up to 127 days in an atmosphere of 99.9% nitrogen at 0 °C.^[139]

Migration

Many beetle species undertake annual mass movements which are termed as migrations. These include the pollen beetle *Meligethes aeneus*^[140] and many species of coccinellids.^[141] These mass movements may also be opportunistic, in search of food, rather than seasonal. A 2008 study of an unusually large outbreak of Mountain Pine Beetle (*Dendroctonus ponderosae*) in British Columbia found that beetles were capable of flying 30–110 km per day in densities of up to 18, 600 beetles per hectare.^[142]

Relationship to humans

In ancient cultures



hpr
in hieroglyphs

Several species of dung beetle, especially the sacred scarab, *Scarabaeus sacer*, were revered in Ancient Egypt.^{[143][144]} The hieroglyphic image of the beetle may have had existential, fictional, or ontologic significance.^[145] Images of the scarab in bone, ivory, stone, Egyptian faience, and precious metals are known from the Sixth Dynasty and up to the period of Roman rule.

The scarab was of prime significance in the funerary cult of ancient Egypt.^[146] The scarab was linked to Khepri, the god of the rising sun, from the supposed resemblance of the rolling of the dung ball by the beetle to the rolling of the sun by the god.^[143] Some of ancient Egypt's neighbors adopted the scarab motif for seals of varying types. The best-known of these are the Judean LMLK seals, where eight of 21 designs contained scarab beetles, which were used exclusively to stamp impressions on storage jars during the reign of Hezekiah.^[147] Beetles are mentioned as a symbol of the sun, as in ancient Egypt, in Plutarch's 1st century *Moralia*.^[148] The Greek Magical Papyri of the 2nd century BC to the 5th century AD describe scarabs as an ingredient in a spell.^[149]



A scarab in the Valley of the Kings

Pliny the Elder discusses beetles in his *Natural History*,^[150] describing the stag beetle: "Some insects, for the preservation of their wings, are covered with a crust (elytra) – the beetle, for instance, the wing of which is peculiarly fine and frail. To these insects a sting has been denied by Nature; but in one large kind we find horns of a remarkable length, two-pronged at the extremities, and forming pincers, which the animal closes when it is its intention to bite."^{[151][152]} The stag beetle is recorded in a Greek myth by Nicander and recalled by Antoninus Liberalis in which Cerambus^[b] is turned into a beetle: "He can be seen on trunks and has hook-teeth, ever moving his jaws together. He is black, long and has hard wings like a great dung beetle".^[153] The story concludes with the comment that the beetles were used as toys by young boys, and that the head was removed and worn as a pendant.^{[152][154]}

As pests



Cotton boll weevil

About 75% of beetle species are phytophagous in both the larval and adult stages. Many feed on economically important plants and stored plant products, including trees, cereals, tobacco, and dried fruits.^[6] Some, such as the boll weevil, which feeds on cotton buds and flowers, can cause extremely serious damage to agriculture. The boll weevil crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico around 1892,^[155] and had reached southeastern Alabama by 1915. By the mid-1920s, it had entered all cotton-growing regions in the US, traveling 40 to 160 miles (60–260 km) per year. It remains the most destructive cotton pest in North America. Mississippi State University has estimated, since the boll weevil entered the United States, it has cost cotton producers about \$13 billion, and in recent times about \$300 million per year.^[155]

The bark beetle, elm leaf beetle and the Asian longhorned beetle (*Anoplophora glabripennis*)^[156] are among the species that attack elm trees. Bark beetles (Scolytidae) carry Dutch elm disease as they move from infected breeding sites to healthy trees. The disease has devastated elm trees across Europe and North America.^[157]

Some species of beetle have evolved immunity to insecticides. For example, the Colorado potato beetle, *Leptinotarsa decemlineata*, is a destructive pest of potato plants. Its hosts include other members of the Solanaceae, such as nightshade, tomato, eggplant and capsicum, as well as the potato. Different populations have between them developed resistance to all major classes of insecticide.^[158] The Colorado potato beetle was evaluated as a tool of entomological warfare during World War II, the idea being to use the beetle and its larvae to damage the crops of enemy nations.^[159] Germany tested its Colorado potato beetle weaponisation program south of Frankfurt, releasing 54,000 beetles.^[160]



Larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*, a serious crop pest

The death watch beetle, *Xestobium rufovillosum* (Ptinidae), is a serious pest of older wooden buildings in Europe. It attacks hardwoods such as oak and chestnut, always where some fungal decay has taken or is taking place. The actual introduction of the pest into buildings is thought to take place at the time of construction.^[161]

Other pests include the coconut hispine beetle, *Brontispa longissima*, which feeds on young leaves, seedlings and mature coconut trees, causing serious economic damage in the Philippines.^[162] The mountain pine beetle is a destructive pest of mature or weakened lodgepole pine, sometimes affecting large areas of Canada.^[163]

As beneficial resources

Beetles can be beneficial to human economics by controlling the populations of pests. The larvae and adults of some species of lady beetles (Coccinellidae) feed on aphids that are pests. Other lady beetles feed on scale insects, whitefly and mealybugs.^[164] If normal food sources are scarce, they may feed on small caterpillars, young plant bugs, or honeydew and nectar.^[165] Ground beetles (Carabidae) are common predators of many insect pests, including fly eggs, caterpillars, and wireworms.^[166] Ground beetles can help to control weeds by eating their seeds in the soil, reducing the need for herbicides to protect crops.^[167] The effectiveness of some species in reducing certain



Coccinella septempunctata, a predatory beetle beneficial to agriculture

plant populations has resulted in the deliberate introduction of beetles in order to control weeds. For example, the genus *Zygogramma* is native to North America but has been used to control *Parthenium hysterophorus* in India and *Ambrosia artemisiifolia* in Russia.^{[168][169]}

Dung beetles (Scarabidae) have been successfully used to reduce the populations of pestilent flies, such as *Musca vetustissima* and *Haematobia exigua* which are serious pests of cattle in Australia.^[170] The beetles make the dung unavailable to breeding pests by quickly rolling and burying it in the soil, with the added effect of improving soil fertility, tilth, and nutrient cycling.^[171] The Australian Dung Beetle Project (1965–1985), introduced species of dung beetle to Australia from South Africa and Europe to reduce populations of *Musca vetustissima*, following successful trials of this technique in Hawaii.^[170] The American Institute of Biological Sciences reports that dung beetles save

the United States cattle industry an estimated US\$380 million annually through burying above-ground livestock feces.^[172]

The Dermestidae are often used in taxidermy and in the preparation of scientific specimens, to clean soft tissue from bones.^[173] Larvae feed on and remove cartilage along with other soft tissue.^{[174][175]}

As food and medicine

Beetles are the most widely eaten insects, with about 344 species used as food, usually at the larval stage.^[176] The mealworm (the larva of the darkling beetle) and the rhinoceros beetle are among the species commonly eaten.^[177] A wide range of species is also used in folk medicine to treat those suffering from a variety of disorders and illnesses, though this is done without clinical studies supporting the efficacy of such treatments.^[178]



Mealworms in a bowl for human consumption

As biodiversity indicators

Due to their habitat specificity, many species of beetles have been suggested as suitable as indicators, their presence, numbers, or absence providing a measure of habitat quality. Predatory beetles such as the tiger beetles (Cicindelidae) have found scientific use as an indicator taxon for measuring regional patterns of biodiversity. They are suitable for this as their taxonomy is stable; their life history is well described; they are large and simple to observe when visiting a site; they occur around the world in many habitats, with species specialised to particular habitats; and their occurrence by species accurately indicates other species, both vertebrate and invertebrate.^[179] According to the habitats, many other groups such as the rove beetles in human-modified habitats, dung beetles in savannas^[180] and saproxylic beetles in forests^[181] have been suggested as potential indicator species.^[182]

In art and adornment

Many beetles have beautiful and durable elytra that have been used as material in arts, with beetlewing the best example.^[183] Sometimes, they are incorporated into ritual objects for their religious significance. Whole beetles, either as-is or encased in clear plastic, are made into objects ranging from cheap souvenirs such as key chains to expensive fine-art jewellery. In parts of Mexico, beetles of the genus *Zopherus* are made into living brooches by attaching costume jewelry and golden chains, which is made possible by the incredibly hard elytra and sedentary habits of the genus.^[184]



Zopheridae in jewellery at the Texas A&M University Insect Collection

In entertainment



Pendant watch in shape of beetle, Switzerland 1850-1900 gold, diamond, enamel

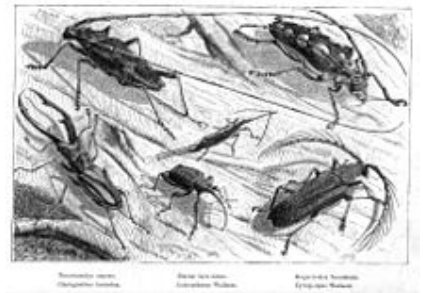
Fighting beetles are used for entertainment and gambling. This sport exploits the territorial behavior and mating competition of certain species of large beetles. In the Chiang Mai district of northern Thailand, male *Xylotrupes rhinoceros* beetles are caught in the wild and trained for fighting. Females are held inside a log to stimulate the fighting males with their pheromones.^[185] These fights may be competitive and involve gambling both money and property.^[186] In South Korea the Dytiscidae species *Cybister tripunctatus* is used in a roulette-like game.^[187]

Beetles are sometimes used as instruments: the Onabasulu of Papua New Guinea historically used the weevil *Rhynchophorus ferrugineus* as a musical instrument by letting the human mouth serve as a variable resonance chamber for the wing vibrations of the live adult beetle.^[186]

As pets

Some species of beetle are kept as pets, for example diving beetles (Dytiscidae) may be kept in a domestic fresh water tank.^[188]

In Japan the practice of keeping horned rhinoceros beetles (Dynastinae) and stag beetles (Lucanidae) is particularly popular amongst young boys.^[189] Such is the popularity in Japan that vending machines dispensing live beetles were developed in 1999, each holding up to 100 stag beetles.^{[190][191]}



"Remarkable Beetles Found at Simunjon, Borneo".^[c] A few of the 2000 species of beetle collected by Alfred Russel Wallace in Borneo

As things to collect

Beetle collecting became extremely popular in the Victorian era.^[192] The naturalist Alfred Russel Wallace collected (by his own count) a total of 83,200 beetles during the eight years described in his 1869 book *The Malay Archipelago*, including 2,000 species new to science.^[193]

As inspiration for technologies

Several coleopteran adaptations have attracted interest in biomimetics with possible commercial applications. The bombardier beetle's powerful repellent spray has inspired the development of a fine mist spray technology, claimed to have a low carbon impact compared to aerosol sprays.^[194] Moisture harvesting behavior by the Namib desert beetle (*Stenocara gracilipes*) has inspired a self-filling water bottle which utilises hydrophilic and hydrophobic materials to benefit people living in dry regions with no regular rainfall.^[195]

Living beetles have been used as cyborgs. A Defense Advanced Research Projects Agency funded project implanted electrodes into *Mecynorhina torquata* beetles, allowing them to be remotely controlled via a radio receiver held on its back, as proof-of-concept for surveillance work.^[196] Similar technology has been applied to enable a human operator to control the free-flight steering and walking gaits of *Mecynorhina torquata* as well as graded turning and backward walking of *Zophobas morio*.^{[197][198][199]}

In conservation

Since beetles form such a large part of the world's biodiversity, their conservation is important, and equally, loss of habitat and biodiversity is essentially certain to impact on beetles. Many species of beetles have very specific habitats and long life cycles that make them vulnerable. Some species are highly threatened while others are already feared extinct.^[200] Island species tend to be more susceptible as in the case of *Helictopleurus undatus* of Madagascar which is thought to have gone extinct during the late 20th century.^[201] Conservationists have attempted to arouse a liking for beetles with flagship species like the stag beetle, *Lucanus cervus*,^[202] and tiger beetles (Cicindelidae). In Japan the Genji firefly, *Luciola cruciata*, is extremely popular, and in South Africa the Addo elephant dung beetle offers promise for broadening ecotourism beyond the big five tourist mammal species. Popular dislike of pest beetles, too, can be turned into public interest in insects, as can unusual ecological adaptations of species like the fairy shrimp hunting beetle, *Cicinis bruchi*.^[203]

Bed bug

Bed bugs are a type of insect that feed on human blood, usually at night.^[7] Their bites can result in a number of health impacts including skin rashes, psychological effects and allergic symptoms.^[5] Bed bug bites may lead to skin changes ranging from invisible to small areas of redness to prominent blisters.^{[1][2]} Symptoms may take between minutes to days to appear and itchiness is generally present.^[2] Some individuals may feel tired or have a fever.^[2] Typically, uncovered areas of the body are affected and often three bites occur in a row.^[2] Bed bugs bites are not known to transmit any infectious disease.^{[5][7]} Complications may rarely include areas of dead skin or vasculitis.^[2]

Bed bug bites are caused primarily by two species of insects of the *Cimex* type: *Cimex lectularius* (the common bed bug) and *Cimex hemipterus*, primarily in the tropics.^[3] Their size ranges between 1 and 7 mm.^[7] They spread by crawling between nearby locations or by being carried within personal items.^[2] Infestation is rarely due to a lack of hygiene but is more common in high-density areas.^{[2][8]} Diagnosis involves both finding the bugs and the occurrence of compatible symptoms.^[5] Bed bugs spend much of their time in dark, hidden locations like mattress seams or cracks in the wall.^[2]

Treatment is directed towards the symptoms.^[2] Eliminating bed bugs from the home is often difficult, partly because bed bugs can survive up to a year without feeding.^[2] Repeated treatments of a home may be required.^[2] These treatments may include heating the room to 50 °C (122 °F) for more than 90 minutes, frequent vacuuming, washing clothing at high temperatures, and the use of various pesticides.^[2]

Bed bugs occur in all regions of the globe.^[7] Rates of infestations are relatively common, following an increase since the 1990s.^{[3][4][6]} The exact causes of this increase are unclear; theories including increased human travel, more frequent exchange of second-hand furnishings, a greater focus on control of other pests, and increasing resistance to pesticides.^[4] Bed bugs have been known human parasites for thousands of years.^[2]

Bed bugs	
Other names	Cimicosis, bed bug bites, bedbugs, bed bug infestation
	
An adult bed bug (<i>Cimex lectularius</i>) with the typical flattened oval shape	
Specialty	Family medicine, dermatology
Symptoms	None to prominent blisters, itchy ^{[1][2]}
Usual onset	Minutes to days after the bite ^[2]
Causes	<i>Cimex</i> (primarily <i>Cimex lectularius</i> and <i>Cimex hemipterus</i>) ^[3]
Risk factors	Travel, second-hand furnishings ^[4]
Diagnostic method	Based on finding bed bugs and symptoms ^[5]
Differential diagnosis	Allergic reaction, scabies, dermatitis herpetiformis ^[2]
Treatment	Symptomatic, bed bug eradication ^[2]
Medication	Antihistamines, corticosteroids ^[2]
Frequency	Relatively common ^[6]

Contents

Signs and symptoms

- Skin
- Psychological
- Other

Insect

- Spread

Diagnosis

- Detection
- Differential diagnosis

Prevention

Management

Epidemiology

- Species

History

- 20th century

Society and culture

- Legal action
- Literature

Research

References

External links

Signs and symptoms

Skin

Individual responses to bites vary, ranging from no visible effect (in about 20–70%),^{[3][5]} to small macular spots, to prominent wheals and bullae formations along with intense itching that may last several days.^[5] The bites often occur in a line. A central spot of bleeding may also occur due to the release of anticoagulants in the bug's saliva.^[4]

Symptoms may not appear until some days after the bites have occurred.^[5] Reactions often become more brisk after multiple bites due to possible sensitization to the salivary proteins of the bed bug.^[3] The skin reaction usually occurs in the area of the bite which is most commonly the arms, shoulders and legs as they are more frequently exposed at night.^[5] Numerous bites may lead to an erythematous rash or urticaria.^[5]



Bedbug bites

Psychological

Serious infestations and chronic attacks can cause anxiety, stress, and insomnia.^[5] Development of refractory delusional parasitosis is possible, as a person develops an overwhelming obsession with bed bugs.^[9]

Other

A number of other symptoms may occur from either the bite of the bed bugs or from their exposure. Anaphylaxis from the injection of serum and other nonspecific proteins has been rarely documented.^{[5][10]} Due to each bite taking a tiny amount of blood, chronic or severe infestation may lead to anemia.^[5] Bacterial skin infection may occur due to skin break down from scratching.^{[5][11]} Systemic poisoning may occur if the bites are numerous.^[12] Exposure to bed bugs may trigger an asthma attack via the effects of airborne allergens although evidence of this association is limited.^[5] There is no evidence that bed bugs transmit infectious diseases^{[5][7]} even though they appear physically capable of carrying pathogens and this possibility has been investigated.^{[3][5]} The bite itself may be painful thus resulting in poor sleep and worse work performance.^[5]

Similar to humans, pets can also be bitten by bed bugs. The signs left by the bites are the same as in case of people and cause identical symptoms (skin irritation, scratching etc).



Bedbug bites

Insect

Bed bug infestations are primarily the result of two species of insects from genus *Cimex*: *Cimex lectularius* (the common bed bug) and *Cimex hemipterus*.^[3] These insects feed exclusively on blood and may survive a year without eating.^[3] Adult *Cimex* are light brown to reddish-brown, flat, oval, and have no hind wings. The front wings are vestigial and reduced to pad-like structures. Adults grow to 4–5 mm (0.16–0.20 in) long and 1.5–3 mm (0.059–0.118 in) wide.

Bed bugs have five immature nymph life stages and a final sexually mature adult stage.^[13] They shed their skins through ecdysis at each stage, discarding their outer exoskeleton.^[14] Newly hatched nymphs are translucent, lighter in color, and become browner as they moult and reach maturity. Bed bugs may be mistaken for other insects, such as booklice, small cockroaches, or carpet beetles; however, when warm and active, their movements are more ant-like, and like most other true bugs, they emit a characteristic disagreeable odor when crushed.

Bed bugs are obligatory bloodsuckers. They have mouth parts that saw through the skin and inject saliva with anticoagulants and painkillers. Sensitivity of humans varies from extreme allergic reaction to no reaction at all (about 20%). The bite usually produces swelling with no red spot, but when many bugs feed on a small area, reddish spots may appear after the swelling subsides.^[15] Bedbugs prefer exposed skin, preferably the face, neck, and arms of a sleeping person.

Bed bugs are attracted to their hosts primarily by carbon dioxide, secondarily by warmth, and also by certain chemicals.^{[4][16][17][18]} *Cimex lectularius* only feeds every five to seven days, which suggests that it does not spend the majority of its life searching for a host. When a bed bug is starved, it leaves its shelter and searches for a host. It returns to its shelter after successful feeding or if it encounters exposure to light.^[19] *Cimex lectularius* aggregate under all life stages and mating conditions. Bed bugs may choose to aggregate because of predation, resistance to desiccation, and more opportunities to find a mate. Airborne pheromones are responsible for aggregations.^[20]



An adult bed bug is about 4 to 5 mm long.

Spread

Infestation is rarely caused by a lack of hygiene.^[8] Transfer to new places is usually in the personal items of the human they feed upon.^[3] Dwellings can become infested with bed bugs in a variety of ways, such as:

- Bugs and eggs inadvertently brought in from other infested dwellings on a visiting person's clothing or luggage;
- Infested items (such as furniture especially beds or couches, clothing, or backpacks) brought in a home or business;
- Proximity of infested dwellings or items, if easy routes are available for travel, e.g. through ducts or false ceilings;
- Wild animals (such as bats or birds)^{[21][22]} that may also harbour bed bugs or related species such as the bat bug;
- People visiting an infested area (e.g. dwelling, means of transport, entertainment venue, or lodging) and carrying the bugs to another area on their clothing, luggage, or bodies. Bedbugs are increasingly found in air travel.^[23]

Though bed bugs will opportunistically feed on pets, they do not live or travel on the skin of their hosts, and pets are not believed to be a factor in their spread.^[24]

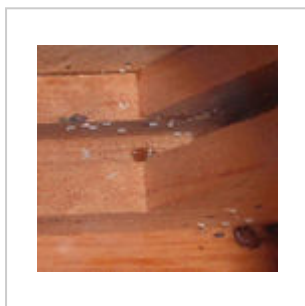
Diagnosis

A definitive diagnosis of health effects due to bed bugs requires a search for and finding of the insect in the sleeping environment as symptoms are not sufficiently specific.^[5] Bed bugs classically form a line of bites colloquially referred to as "breakfast, lunch, and dinner" and rarely feed in the armpit or behind the knee which may help differentiate it from other biting insects.^[4] If the number in a house is large a pungent sweet odor may be described.^[4] There are specially trained dogs that can detect this smell.^[2]

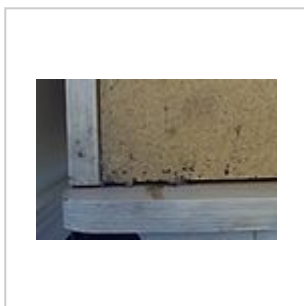
Detection

Bed bugs can exist singly, but tend to congregate once established. Although strictly parasitic, they spend only a tiny fraction of their lifecycles physically attached to hosts. Once a bed bug finishes feeding, it relocates to a place close to a known host, commonly in or near beds or couches in clusters of adults, juveniles, and eggs—which entomologists call harborage areas or simply harborages to which the insect returns after future feedings by following chemical trails. These places can vary greatly in format, including luggage, inside of vehicles, within furniture, among bedside clutter—even inside electrical sockets and nearby laptop computers. Bed bugs may also nest near animals that have nested within a dwelling, such as bats, birds,^[22] or rodents. They are also capable of surviving on domestic cats and dogs, though humans are the preferred host of *C. lectularius*.^[25]

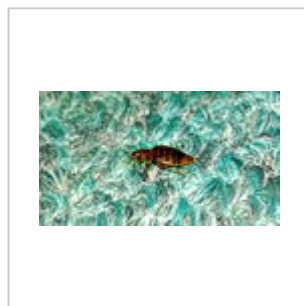
Bed bugs can also be detected by their characteristic smell of rotting raspberries.^[26] Bed bug detection dogs are trained to pinpoint infestations, with a possible accuracy rate between 11% and 83%.^[6] Homemade detectors have been developed.^{[27][28]}



Eggs and two adults found inside a dresser



Fecal spot



Bed bug on carpet

Differential diagnosis

Other possible conditions with which these conditions can be confused include scabies, gamasoidosis, allergic reactions, mosquito bites, spider bites, chicken pox and bacterial skin infections.^[5]

Prevention

To prevent bringing home bed bugs, travelers are advised to take precautions after visiting an infested site: generally, these include checking shoes on leaving the site, changing clothes outside the house before entering, and putting the used clothes in a clothes dryer outside the house. When visiting a new lodging, it is advised to check the bed before taking suitcases into the sleeping area, and putting the suitcase on a raised stand to make bedbugs less likely to crawl in. An extreme measure would be putting the suitcase in the tub. Clothes should be hung up or left in the suitcase, and never left on the floor.^[29] The founder of a company dedicated to bedbug extermination said that 5% of hotel rooms he books into were infested. He advised people never to sit down on public transport; check office chairs, plane seats, and hotel mattresses; and monitor and vacuum home beds once a month.^[30]

Management

Treatment requires keeping the person from being repeatedly bitten and possible symptomatic use of antihistamines and corticosteroids (either topically or systemically).^[5] There however is no evidence that medications improve outcomes and symptoms usually resolve without treatment in 1–2 weeks.^{[3][4]}

Avoiding repeated bites can be difficult, since it usually requires eradicating bed bugs from a home or workplace; eradication frequently requires a combination of pesticide and non-pesticide approaches.^[3] Pesticides that have historically been found to be effective include pyrethroids, dichlorvos and malathion.^[4] Resistance to pesticides has increased significantly over time and there are concerns of negative health effects from their use.^[3] Mechanical approaches, such as vacuuming up the insects and heat-treating or wrapping mattresses have been recommended.^[3]

Once established, bed bugs are extremely difficult to get rid of.^[3] This frequently requires a combination of nonpesticide approaches and the use of insecticides.^{[3][4]}

Mechanical approaches, such as vacuuming up the insects and heat-treating or wrapping mattresses, are effective.^{[3][6]} An hour at a temperature of 45 °C (113 °F) or over, or two hours at less than −17 °C (1 °F) kills them.^[6] This may include a domestic clothes drier for fabric or a commercial steamer. Bed bugs and their eggs will die on contact when exposed to surface temperatures above 180 °F (82 °C) and a steamer can reach well above 230 °F (110 °C).^{[15][31]} A study found 100% mortality rates for bed bugs exposed to temperatures greater than 50 °C (122 °F) for more than 2 minutes. The study recommended maintaining temperatures of above 48 °C (118 °F) for more than 20 min to effectively kill all life stages of bed bugs, and because in practice treatment times of 6 to 8 hours are used to account for cracks and indoor clutter.^[32] This method is expensive and has caused fires.^{[6][15]} Starving bedbugs is not effective, as they can survive without eating for 100 to 300 days, depending on temperature.^[6]

It was stated in 2012 that no truly effective insecticides were available.^[6] Insecticides that have historically been found effective include pyrethroids, dichlorvos, and malathion.^[4] Resistance to pesticides has increased significantly in recent decades, and harm to health from their use is of concern.^[3] The carbamate insecticide propoxur is highly toxic to bed bugs, but it has potential toxicity to children exposed to it, and the US Environmental Protection Agency has been reluctant to approve it for indoor use.^[33] Boric acid, occasionally applied as a safe indoor insecticide, is not effective against bed bugs^[34] because they do not groom.^[35]

Epidemiology

Bed bugs occur around the world.^[36] Before the 1950s about 30% of houses in the United States had bedbugs.^[2] Rates of infestation in developed countries, while decreasing from the 1930s to the 1980s, have increased dramatically since the 1980s.^{[3][4][36]} This is believed to be partly due to the use of DDT to kill cockroaches.^[37] The invention of the vacuum cleaner and simplification of furniture design may have also played a role.^[37] Others believe it might simply be the cyclical nature of the organism.^[38]

The dramatic increase in bedbug populations in the developed world, which began in the 1980s, is thought to be due to greater foreign travel, increased immigration from the developing world to the developed world, more frequent exchange of second-hand furnishings among homes, a greater focus on control of other pests, resulting in neglect of bed bug countermeasures, and increasing bedbug resistance to pesticides.^{[4][39]} Lower cockroach populations due to insecticide use may have aided bed bugs' resurgence, since cockroaches are known to sometimes predate them.^[40] Bans on DDT and other potent pesticides may have also contributed.^{[41][42]}

The U.S. National Pest Management Association reported a 71% increase in bed bug calls between 2000 and 2005.^[43] The number of reported incidents in New York City alone rose from 500 in 2004 to 10,000 in 2009.^[44] In 2013, Chicago was listed as the number 1 city in the United States for bedbug infestations.^[45] As a result, the Chicago City Council passed a bed bug control ordinance to limit their spread. Additionally, bed bugs are reaching places in which they never established before, such as southern South America.^{[46][47]}

The rise in infestations has been hard to track because bed bugs are not an easily identifiable problem and is one that people prefer not to discuss. Most of the reports are collected from pest-control companies, local authorities, and hotel chains.^[48] Therefore, the problem may be more severe than is currently believed.^[49]

Species

The common bed bug (*C. lectularius*) is the species best adapted to human environments. It is found in temperate climates throughout the world. Other species include *Cimex hemipterus*, found in tropical regions, which also infests poultry and bats, and *Leptocimex boueti*, found in the tropics of West Africa and South America, which infests bats and humans. *Cimex pilosellus* and *Cimex pipistrella* primarily infest bats, while *Haematosiphon inodora*, a species of North America, primarily infests poultry.^[50]

History

Cimicidae the ancestor of modern bed bugs first emerged approximately 115 million years ago, more than 30 million years before bats, their previously presumed initial host first appeared. From unknown ancestral hosts, a variety of different lineages evolved which specialized in either bats or birds. The common (*C. lectularius*) and tropical bed bug (*C. hemipterus*), split 40 million years before *Homo* evolution. Humans became hosts to bed bugs through host specialist extension (rather than switching) on three separate occasions.^{[51][52]}

Bed bugs were mentioned in ancient Greece as early as 400 BC, and were later mentioned by Aristotle. Pliny's *Natural History*, first published circa AD 77 in Rome, claimed bed bugs had medicinal value in treating ailments such as snake bites and ear infections. Belief in the medicinal use of bed bugs persisted until at least the 18th century, when Guettard recommended their use in the treatment of hysteria.^[53]

Bed bugs were first mentioned in Germany in the 11th century, in France in the 13th century, and in England in 1583,^[54] though they remained rare in England until 1670. Some in the 18th century believed bed bugs had been brought to London with supplies of wood to rebuild the city after the Great Fire of London (1666). Giovanni Antonio Scopoli noted their presence in Carniola (roughly equivalent to present-day Slovenia) in the 18th century.^{[55][56]}

Traditional methods of repelling and/or killing bed bugs include the use of plants, fungi, and insects (or their extracts), such as black pepper;^[57] black cohosh (*Actaea racemosa*); *Pseudarthria hookeri*; *Laggera alata* (Chinese *yángmáo cǎo* | 羊毛草);^[15] *Eucalyptus saligna* oil;^{[58][59]} henna (*Lawsonia inermis* or camphire);^[60] "infused oil of *Melolontha vulgaris*" (presumably cockchafer); fly agaric (*Amanita muscaria*); tobacco; "heated oil of Terebinthina" (i.e. true turpentine); wild mint (*Mentha arvensis*); narrow-leaved pepperwort (*Lepidium ruderales*); *Myrica* spp. (e.g. bayberry); Robert geranium (*Geranium robertianum*); bugbane (*Cimicifuga* spp.); "herb and seeds of *Cannabis*"; "opulus" berries (possibly maple or European cranberrybush); masked hunter bugs (*Reduvius personatus*), "and many others".^[61]

In the mid-19th century, smoke from peat fires was recommended as an indoor domestic fumigant against bed bugs.^[62]

Dusts have been used to ward off insects from grain storage for centuries, including plant ash, lime, dolomite, certain types of soil, and diatomaceous earth or Kieselguhr.^[63] Of these, diatomaceous earth in particular has seen a revival as a nontoxic (when in amorphous form) residual pesticide for bed bug abatement. While diatomaceous earth often performs poorly, silica gel may be effective.^{[64][65]}

Basket-work panels were put around beds and shaken out in the morning in the UK and in France in the 19th century. Scattering leaves of plants with microscopic hooked hairs around a bed at night, then sweeping them up in the morning and burning them, was a technique reportedly used in Southern Rhodesia and in the Balkans.^[66]

Bean leaves have been used historically to trap bedbugs in houses in Eastern Europe. The trichomes on the bean leaves capture the insects by impaling the feet (tarsi) of the insects. The leaves are then destroyed.^[67]

20th century

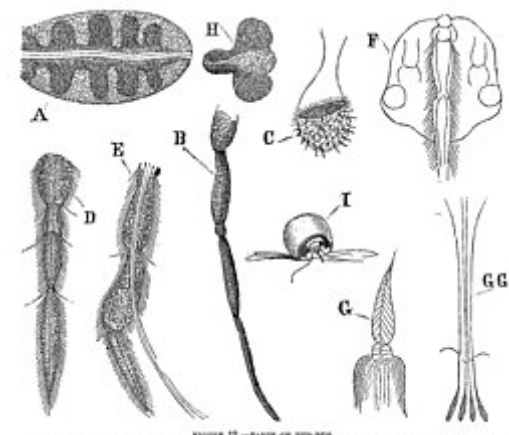
Before the mid-20th century, bed bugs were very common. According to a report by the UK Ministry of Health, in 1933, all the houses in many areas had some degree of bed bug infestation.^[48] The increase in bed bug populations in the early 20th century has been attributed to the advent of electric heating, which allowed bed bugs to thrive year-round instead of only in warm weather.^[68]

Bed bugs were a serious problem at US military bases during World War II.^[69] Initially, the problem was solved by fumigation, using Zyklon Discoids that released hydrogen cyanide gas, a rather dangerous procedure.^[69] Later, DDT was used to good effect.^[69]

The decline of bed bug populations in the 20th century is often credited to potent pesticides that had not previously been widely available.^[70] Other contributing factors that are less frequently mentioned in news reports are increased public awareness and slum clearance programs that combined pesticide use with steam disinfection, relocation of slum dwellers to new housing, and in



1870s–1890s advertisement for a bed bug exterminator. It reads "Use Getz cockroach and bed bug exterminators, sold by all druggists."



1860 engraving of bed bug parts: A. Intestines – B. Antenna of the male – C. Eye – D. Haustellum, or sucker, closed – E. Side view of sucker – F. Under part of head – G. Under lip – GG. Hair of the tube, and outside cases – H. Egg-bag – I. Larva emerging from the eggs

some cases also follow-up inspections for several months after relocated tenants moved into their new housing.^[68]

Society and culture

Legal action

Bed bugs are an increasing cause for litigation.^[71] Courts have, in some cases, exacted large punitive damage judgments on some hotels.^{[72][73][74]} Many of New York City's Upper East Side homeowners have been afflicted, but they tend to remain publicly silent in order not to ruin their property values and be seen as suffering a blight typically associated with the lower classes.^[75] Local Law 69 in New York City requires owners of buildings with three or more units to provide their tenants and potential tenants with reports of bedbug history in each unit. They must also prominently post these listings and reports in their building.^[76]

Literature

- "Good night, sleep tight, don't let the bed bugs bite," is a traditional saying.^[77]
- *The Bedbug* (Russian: Клоп, Klop) is a play by Vladimir Mayakovsky written in 1928–1929.

Research

Bed bug secretions can inhibit the growth of some bacteria and fungi; antibacterial components from the bed bug could be used against human pathogens, and be a source of pharmacologically active molecules as a resource for the discovery of new drugs.^[78]

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Moth

Moths are a polyphyletic group of insects that includes all members of the order Lepidoptera that are not butterflies, with moths making up the vast majority of the order. There are thought to be approximately 160,000 species of moth,^[1] many of which have yet to be described. Most species of moth are nocturnal, but there are also crepuscular and diurnal species.

Contents

Differences between butterflies and moths

Etymology

Caterpillar

History

Economics

Significance to humans

Predators and parasites

Ecological importance

Attraction to light



Noteworthy moths

Moths of economic significance

Gallery

See also

References

Moths	
	
Emperor gum moth, <i>Opodiphthera eucalypti</i>	
Scientific classification 	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
(unranked):	Heterocera

Differences between butterflies and moths

While the butterflies form a monophyletic group, the moths, comprising the rest of the Lepidoptera, do not. Many attempts have been made to group the superfamilies of the Lepidoptera into natural groups, most of which fail because one of the two groups is not monophyletic: Microlepidoptera and Macrolepidoptera, Heterocera and Rhopalocera, Jugatae and Frenatae, Monotrysia and Ditrysia.^[2]

Although the rules for distinguishing moths from butterflies are not well established, one very good guiding principle is that butterflies have thin antennae and (with the exception of the family Hedyliidae) have small balls or clubs at the end of their antennae. Moth antennae are usually feathery with no ball on the end. The divisions are named by this principle: "club-antennae" (Rhopalocera) or "varied-antennae" (Heterocera).

Etymology

The modern English word "moth" comes from Old English "*moððe*" (cf. Northumbrian "*mohðe*") from Common Germanic (compare Old Norse "*motti*", Dutch "*mot*", and German "*Motte*" all meaning "moth"). Its origins are possibly related to the Old English "*maða*" meaning "maggot" or from the root of "midge" which until the 16th century was used mostly to indicate the larva, usually in reference to devouring clothes.

Caterpillar



Poplar hawk-moth caterpillar
(*Laothoe populi*)

Moth larvae, or caterpillars, make cocoons from which they emerge as fully grown moths with wings. Some moth caterpillars dig holes in the ground, where they live until they are ready to turn into adult moths.^[3]

History

Moths evolved long before butterflies, with fossils having been found that may be 190 million years old. Both types of Lepidoptera are thought to have evolved along with flowering



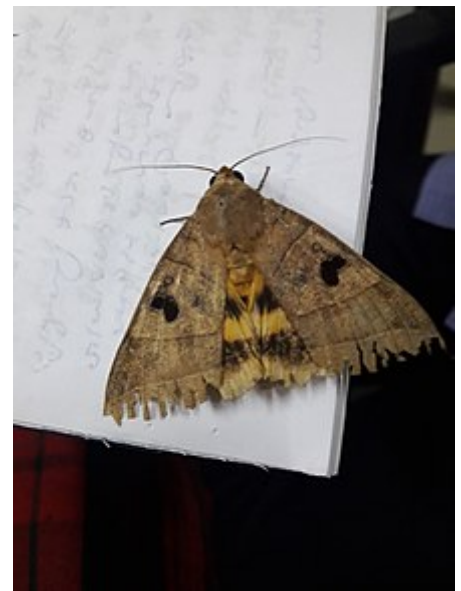
Moth larva from India

plants, mainly because most modern species feed on flowering plants, both as adults and larvae. One of the earliest species thought to be a moth-ancestor is *Archaeolepis mane*, whose fossil fragments show scaled wings similar to caddisflies in their veining.^[4]

Economics

Significance to humans

Some moths, particularly their caterpillars, can be major agricultural pests in many parts of the world. Examples include corn borers and bollworms.^[5] The caterpillar of the gypsy moth (*Lymantria dispar*) causes severe damage to forests in the northeastern United States, where it is an invasive species. In temperate climates, the codling moth causes extensive damage, especially to fruit farms. In tropical and subtropical climates, the diamondback moth (*Plutella xylostella*) is perhaps the most serious pest of brassicaceous crops. Also in sub-Saharan Africa, the African sugarcane borer is a major pest of sugarcane, maize, and sorghum.^[6]



Moth from Kerala, India

Several moths in the family Tineidae are commonly regarded as pests because their larvae eat fabric such as clothes and blankets made from natural proteinaceous fibers such as wool or silk.^[7] They are less likely to eat mixed materials containing some artificial fibers. There are some reports that they may be repelled by the scent of wood from juniper and cedar, by lavender, or by other natural oils; however, many consider this unlikely to prevent infestation. Naphthalene (the chemical used in mothballs) is considered more effective, but there are concerns over its effects on human health.

Moth larvae may be killed by freezing the items which they infest for several days at a temperature below -8°C (18°F).^[8]

Despite being notorious for eating clothing, most moth adults do not eat at all. Many, like the Luna, Polyphemus, Atlas, Promethea, cecropia, and other large moths do not have mouth parts. While there are many species of adult moths that do eat, there are many that will drink nectar.^[7]

Some moths are farmed for their economic value. The most notable of these is the silkworm, the larva of the domesticated moth *Bombyx mori*. It is farmed for the silk with which it builds its cocoon. As of 2002, the silk industry produces more than 130 million kilograms of raw silk, worth about 250 million U.S. dollars, each year.^{[9][10][11]}

Not all silk is produced by *Bombyx mori*. There are several species of Saturniidae that also are farmed for their silk, such as the ailanthus moth (*Samia cynthia* group of species), the Chinese oak silkmoth (*Antheraea pernyi*), the Assam silkmoth (*Antheraea assamensis*), and the Japanese silk moth (*Antheraea yamamai*).

The larvae of many species are used as food, particularly in Africa, where they are an important source of nutrition. The mopane worm, the caterpillar of *Gonimbrasia belina*, from the family Saturniidae, is a significant food resource in southern Africa. Another saturniid used as food is the cavorting emperor (*Usta terpsichore*). In one country alone, Congo, more than 30 species of moth larvae are harvested. Some are sold not only in the local village markets, but are shipped by the ton from one country to another.^[12]

Predators and parasites

Nocturnal insectivores often feed on moths; these include some bats, some species of owls and other species of birds. Moths also are eaten by some species of lizards, amphibians, cats, dogs, rodents, and some bears. Moth larvae are vulnerable to being parasitized by Ichneumonidae.

Baculoviruses are parasite double-stranded DNA insect viruses that are used mostly as biological control agents. They are members of the Baculoviridae, a family that is restricted to insects. Most baculovirus isolates have been obtained from insects, in particular from Lepidoptera.

There is evidence that ultrasound in the range emitted by bats causes flying moths to make evasive maneuvers because bats eat moths. Ultrasonic frequencies trigger a reflex action in the noctuid moth that causes it to drop a few inches in its flight to evade attack.^[13] Tiger moths also emit clicks which can foil bats' echolocation.^{[14][15]}

The fungus *Ophiocordyceps sinensis* infects the larvae of many different species of moths.^[16]

Ecological importance

Some studies indicate that certain species of moths, such as those belonging to the families Erebidæ and Sphingidae, may be the key pollinators for some flowering plants in the Himalayan ecosystem.^{[17][18]}

Attraction to light

Moths frequently appear to circle artificial lights, although the reason for this behavior (positive phototaxis) remains unknown. One hypothesis is called celestial or transverse orientation. By maintaining a constant angular relationship to a bright celestial light, such as the moon, they can fly in a straight line. Celestial objects are so far away that, even after travelling great distances, the change in angle between the moth and the light source is negligible; further, the moon will always be in the upper part of the visual field, or on the horizon. When a moth encounters a much closer artificial light and uses it for navigation, the angle changes noticeably after only a short distance, in addition to being often below the horizon. The moth instinctively attempts to correct by turning toward the light, thereby causing airborne moths to come plummeting downward, and resulting in a spiral flight path that gets closer and closer to the light source.^[19]



An adult male pine processionary moth (*Thaumetopoea pityocampa*). This species is a serious forest pest when in its larval state. Notice the bristle springing from the underside of the hindwing (frenulum) and running forward to be held in a small catch of the forewing, whose function is to link the wings together.



Tomato hornworm parasitized by braconid wasps

Studies have found that light pollution caused by increasing use of artificial lights has either led to a severe decline in moth population in some parts of the world^{[20][21][22]} or has severely disrupted nocturnal pollination.^{[23][24]}

Noteworthy moths

- Atlas moth (*Attacus atlas*), the largest moth in the world
- White witch moth (*Thysania agrippina*), the Lepidopteran with the longest wingspan
- Madagascan sunset moth (*Chrysiridia rhipheus*), considered to be one of the most impressive and beautiful Lepidoptera^[25]
- Death's-head hawkmoth (*Acherontia* spp.), is associated with the supernatural and evil and has been featured in art and movies
- Peppered moth (*Biston betularia*), the subject of a well-known study in natural selection
- Luna moth (*Actias luna*)
- Grease moth (*Aglossa cuprina*), known to have fed on the rendered fat of humans^[26]
- Emperor gum moth (*Opodiphthera eucalypti*)
- Polyphemus moth (*Antheraea polyphemus*)
- Bogong moth (*Agrotis infusa*), known to have been a food source for southeastern indigenous Australians
- Ornate moth (*Utetheisa ornatrix*), the subject of numerous behavioral studies regarding sexual selection



Assorted moths in the University of Texas Insect Collection

Moths of economic significance

- Gypsy moth (*Lymantria dispar*), an invasive species pest of hardwood trees in North America
- Winter moth (*Operophtera brumata*), an invasive species pest of hardwood trees, cranberry and blueberry in northeastern North America
- Corn earworm or cotton bollworm (*Helicoverpa zea*), a major agricultural pest
- Indianmeal moth (*Plodia interpunctella*), a major pest of grain and flour
- Codling moth (*Cydia pomonella*), a pest mostly of apple, pear and walnut trees
- Light brown apple moth (*Epiphyas postvittana*), a highly polyphagous pest
- Silkworm (*Bombyx mori*), for its silk
- Wax moths (*Galleria mellonella*, *Achroia grisella*), pests of bee hives
- *Duponchelia fovealis*, a new invasive pest of vegetables and ornamental plants in the United States

Gallery

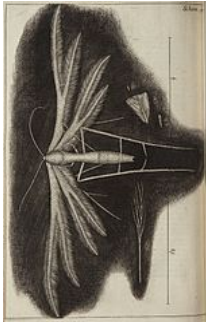


Diagram of a plume moth from Robert Hooke's *Micrographia*



Leaf-shaped moth (*Pergesa acteus*)



Giant grey moth (*Agrius convolvuli*)



Oleander hawk-moth or army green moth (*Daphnis nerii*)



Six-spot burnet moths mating (*Zygaena filipendulae*)



Protective silk (or similar material) case (cocoon)



A caterpillar of death's-head hawkmoth



Mating pair of *Laothoe populi*, or poplar hawkmoths, showing two different color variants



White-lined sphinx moth in Colorado, United States



Closeup of a common clothes moth



Giant silk moth (*Adelowalkeria tristygma*)



Adult emperor moth (*Gonimbrasia belina*)



Sphingidae - Kerala

See also

- Baculovirus
- Butterfly
- Clothing moth
- Comparison of butterflies and moths
- Lepidoptera
- List of moths
- Lepidopterism
- Pollination

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 Evolution of Moths and Butterflies (<http://cdri.org/publications/nature-notes/evolution-ecology/evolution-of-moths-and-butterflies/>) Archived (<https://web.archive.org/web/20140106184057/http://cdri.org/publications/nature-notes/evolution-ecology/evolution-of-moths-and-butterflies/>) 2014-01-06 at the Wayback Machine
 Studying the evolution of butterflies and moths is challenging, since fossils are so rare. But the few Lepidopteran fossils that exist, captured in amber or compressed in fine-grained rocks, show great detail. The earliest Lepidopteran fossils appear in rocks that are about 190 million years old. These tiny fragments of scaled wings and bodies clearly indicate that moths evolved before butterflies.

Ant

Ants are eusocial insects of the family **Formicidae** and, along with the related wasps and bees, belong to the order Hymenoptera. Ants evolved from wasp-like ancestors in the Cretaceous period, about 140 million years ago, and diversified after the rise of flowering plants. More than 12,500 of an estimated total of 22,000 species have been classified.^{[5][6]} They are easily identified by their elbowed antennae and the distinctive node-like structure that forms their slender waists.

Ants form colonies that range in size from a few dozen predatory individuals living in small natural cavities to highly organised colonies that may occupy large territories and consist of millions of individuals. Larger colonies consist of various castes of sterile, wingless females, most of which are workers (ergates), as well as soldiers (dinergates) and other specialised groups.^{[7][8]} Nearly all ant colonies also have some fertile males called "drones" (aner) and one or more fertile females called "queens" (gynes).^[8] The colonies are described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.^{[9][10]}

Ants have colonised almost every landmass on Earth. The only places lacking indigenous ants are Antarctica and a few remote or inhospitable islands. Ants thrive in most ecosystems and may form 15–25% of the terrestrial animal biomass.^[11] Their success in so many environments has been attributed to their social organisation and their ability to modify habitats, tap resources, and defend themselves. Their long co-evolution with other species has led to mimetic, commensal, parasitic, and mutualistic relationships.^[12]

Ant societies have division of labour, communication between individuals, and an ability to solve complex problems.^[13] These parallels with human societies have long been an inspiration and subject of study. Many human cultures make use of ants in cuisine, medication, and rituals. Some species are valued in their role as biological pest control agents.^[14] Their ability to exploit resources may bring ants into conflict with humans, however, as they can damage crops and invade buildings. Some species, such as the red imported fire ant (*Solenopsis invicta*), are regarded as invasive species, establishing themselves in areas where they have been introduced accidentally.^[15]

Contents

- Etymology
- Taxonomy and evolution

Ants	
Temporal range: 140–0 Ma ^[1]	
PreЄ	Є O S D C P T J K PgN
Berriasian – Present	
<div></div>	
A group of fire ants.	
Scientific classification 	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Superfamily:	Formicoidea
Family:	Formicidae <div>Latreille, 1809</div>
Type species	
<i>Formica rufa</i> <div>Linnaeus, 1761</div>	
Subfamilies	

Distribution and diversity

Morphology

- Head
- Mesosoma
- Metasoma
- Polymorphism

Life cycle

- Reproduction

Behaviour and ecology

- Communication
- Defence
- Learning
- Nest construction
- Cultivation of food
- Navigation
- Locomotion
- Cooperation and competition
- Relationships with other organisms

Relationship with humans

- As food
- As pests
- In science and technology
- As pets
- In culture

See also

References

- Cited texts

Further reading

External links

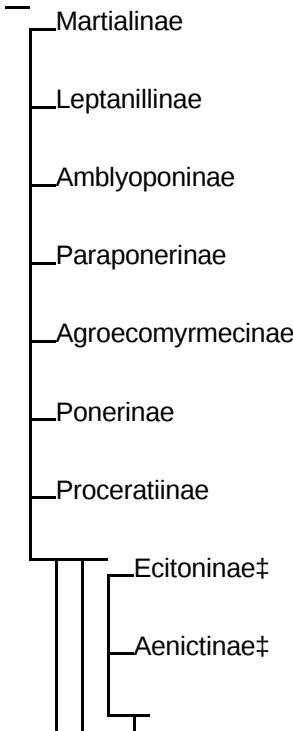
Etymology

The word *ant* and its chiefly dialectal form *emmet*^[16] come from *ante*, *emete* of Middle English, which come from *æmette* of Old English, and these are all related to the dialectal Dutch *emt* and the Old High German *āmeiza*, from which comes the modern German *Ameise*. All of these words come from West Germanic **ǣmaitjōn*, and the original meaning of the word was "the biter" (from Proto-Germanic **ai-*, "off, away" + **mait-* "cut").^{[17][18]} The family name Formicidae is derived from the Latin *formīca* ("ant")^[19] from which the words in other Romance languages, such as the Portuguese *formiga*, Italian *formica*, Spanish *hormiga*, Romanian *furnică*, and French *fourmi* are derived. It has been hypothesised that a Proto-Indo-European word **morwi-* was used, cf. Sanskrit *vamrah*, Latin *formīca*, Greek *μύρμηξ* *mýrmēx*, Old Church Slavonic *mraviji*, Old Irish *moirb*, Old Norse *maurr*, Dutch *mier*.^[20]

Taxonomy and evolution

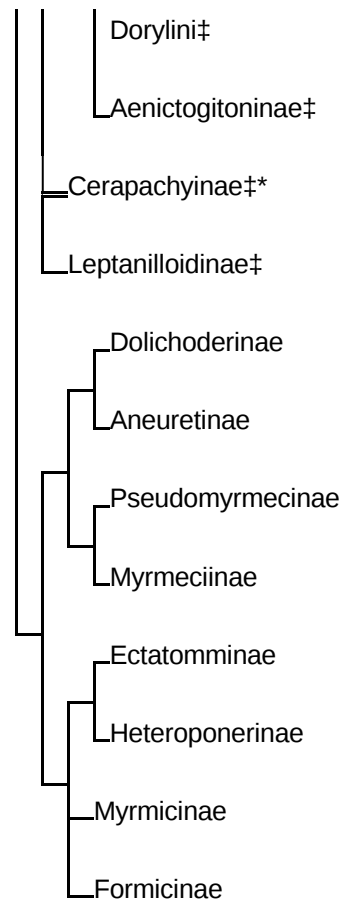
- Agroecomyrmecinae
- Amblyoponinae (incl. "Apomyrminae")
- Aneuretinae
- †Brownimeciinae
- Dolichoderinae
- Dorylinae
- Ectatomminae
- †Formiciinae
- Formicinae
- Heteroponerinae
- Leptanillinae
- Martialinae
- Myrmeciinae (incl. "Nothomyrmeciinae")
- Myrmicinae
- Paraponerinae
- Ponerinae
- Proceratiinae
- Pseudomyrmecinae
- †Sphecomyrminae

Cladogram of subfamilies



The family Formicidae belongs to the order Hymenoptera, which also includes sawflies, bees, and wasps. Ants evolved from a lineage within the stinging wasps, and a 2013 study suggests that they are a sister group of the Apoidea.^[21] In 1966, E. O. Wilson and his colleagues identified the fossil remains of an ant (*Sphecomyrma*) that lived in the Cretaceous period. The specimen, trapped in amber dating back to around 92 million years ago, has features found in some wasps, but not found in modern ants.^[22] *Sphecomyrma* was possibly a ground forager, while *Haidomyrmex* and *Haidomyrmodes*, related genera in subfamily Sphecomyrminae, are reconstructed as active arboreal predators.^[23] Older ants in the genus *Sphecomyrmodes* have been found in 99 million year-old amber from Myanmar.^{[24][25]} A 2006 study suggested that ants arose tens of millions of years earlier than previously thought, up to 168 million years ago.^[1] After the rise of flowering plants about 100 million years ago they diversified and assumed ecological dominance around 60 million years ago.^{[26][1][27][28]} Some groups, such as the Leptanillinae and Martialinae, are suggested to have diversified from early primitive ants that were likely to have been predators underneath the surface of the soil.^{[3][29]}

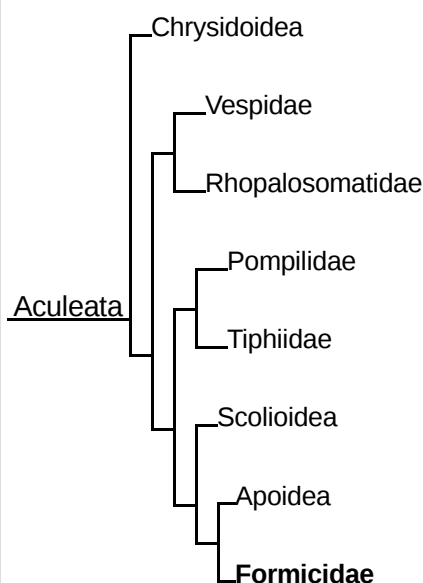
During the Cretaceous period, a few species of primitive ants ranged widely on the Laurasian supercontinent (the Northern Hemisphere). They were scarce in comparison to the populations of other insects, representing only about 1% of the entire insect population. Ants became dominant after adaptive radiation at the beginning of the Paleogene period. By the Oligocene and Miocene, ants had come to represent 20–40% of all insects found in major fossil deposits. Of the species that lived in the Eocene epoch, around one in 10 genera survive to the present. Genera surviving today comprise 56% of the genera in Baltic amber fossils (early Oligocene), and 92% of the genera in Dominican amber fossils (apparently early Miocene).^{[26][30]}



A phylogeny of the extant ant subfamilies.^{[2][3]}

*Cerapachyinae is paraphyletic

† The previous dorylomorph subfamilies were synonymized under Dorylinae by Brady *et al.* in 2014^[4]



Phylogenetic position of the Formicidae.^[21]



Play media
(video) Ants gathering food

Termites live in colonies and are sometimes called ‘white ants’, but termites are not ants. They are the sub-order Isoptera, and together with cockroaches they form the order Blattodea. Blattodeans are related to mantids, crickets, and other winged insects that do not undergo full metamorphosis. Like ants, termites are eusocial, with sterile workers, but they differ greatly in the genetics of reproduction. The similarity of their social structure to that of ants is attributed to convergent evolution.^[31] Velvet ants look like large ants, but are wingless female

wasps.^{[32][33]}

Distribution and diversity

Ants are found on all continents except Antarctica, and only a few large islands, such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species.^{[35][36]} Ants occupy a wide range of ecological niches and exploit many different food resources as direct or indirect herbivores, predators and scavengers. Most ant species are omnivorous generalists, but a few are specialist feeders. Their ecological dominance is demonstrated by their biomass: ants are estimated to contribute

Region	Number of species ^[34]
Neotropics	2,162
Nearctic	580
Europe	180
Africa	2,500
Asia	2,080
Melanesia	275
Australia	985
Polynesia	42



Ants fossilised in Baltic amber

15–20 % (on average and nearly 25% in the tropics) of terrestrial animal biomass, exceeding that of the vertebrates.^[11]

Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in),^{[37][38]} the largest species being the fossil *Titanomyrma giganteum*, the queen of which was 6 centimetres (2.4 in) long with a wingspan of 15 centimetres (5.9 in).^[39] Ants vary in colour; most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 12,000 species are currently known (with upper estimates of the potential existence of about 22,000) (see the article List of ant genera), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants. Online databases of ant species, including AntBase (<http://antbase.org/>) and the Hymenoptera Name Server (<https://hns.osu.edu/>), help to keep track of the known and newly described species.^[40] The relative ease with which ants may be sampled and studied in ecosystems has made them useful as indicator species in biodiversity studies.^{[41][42]}

Morphology

Ants are distinct in their morphology from other insects in having elbowed antennae, metapleural glands, and a strong constriction of their second abdominal segment into a node-like petiole. The head, mesosoma, and metasoma are the three distinct body segments (formally tagmata). The petiole forms a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole may be formed by one or two nodes (the second alone, or the second and third abdominal segments).^[43]

Like other insects, ants have an exoskeleton, an external covering that provides a protective casing around the body and a point of attachment for muscles, in contrast to the internal skeletons of humans and other vertebrates. Insects do not have lungs; oxygen and other gases, such as carbon dioxide, pass through their exoskeleton via tiny valves called spiracles. Insects also lack closed blood vessels; instead, they have a long, thin, perforated tube along the top of the body (called the "dorsal aorta") that functions like a heart, and pumps haemolymph toward the head, thus driving the circulation of the internal fluids. The nervous system consists of a ventral nerve cord that runs the length of the body, with several ganglia and branches along the way reaching into the extremities of the appendages.^[44]

Head

An ant's head contains many sensory organs. Like most insects, ants have compound eyes made from numerous tiny lenses attached together. Ant eyes are good for acute movement detection, but do not offer a high resolution image. They also have three small ocelli (simple eyes) on the top of the head that detect light levels and polarization.^[45] Compared to vertebrates, most ants have poor-to-mediocre eyesight and a few subterranean species are completely blind. However, some ants, such as Australia's

have a distinct bimodal size distribution.^{[50][51]} Some other species show continuous variation in the size of workers. The smallest and largest workers in *Pheidologeton diversus* show nearly a 500-fold difference in their dry-weights.^[52]

Workers cannot mate; however, because of the haplodiploid sex-determination system in ants, workers of a number of species can lay unfertilised eggs that become fully fertile, haploid males. The role of workers may change with their age and in some species, such as honeypot ants, young workers are fed until their gasters are distended, and act as living food storage vessels. These food storage workers are called *repletes*.^[53] For instance, these replete workers develop in the North American honeypot ant *Myrmecocystus mexicanus*. Usually the largest workers in the colony develop into repletes; and, if repletes are removed from the colony, other workers become repletes, demonstrating the flexibility of this particular polymorphism.^[54] This polymorphism in morphology and behaviour of workers initially was thought to be determined by environmental factors such as nutrition and hormones that led to different developmental paths; however, genetic differences between worker castes have been noted in *Acromyrmex* sp.^[55] These polymorphisms are caused by relatively small genetic changes; differences in a single gene of *Solenopsis invicta* can decide whether the colony will have single or multiple queens.^[56] The Australian jack jumper ant (*Myrmecia pilosula*) has only a single pair of chromosomes (with the males having just one chromosome as they are haploid), the lowest number known for any animal, making it an interesting subject for studies in the genetics and developmental biology of social insects.^{[57][58]}



Seven leafcutter ant workers of various castes (left) and two queens (right)

Life cycle

The life of an ant starts from an egg. If the egg is fertilised, the progeny will be female diploid; if not, it will be male haploid. Ants develop by complete metamorphosis with the larva stages passing through a pupal stage before emerging as an adult. The larva is largely immobile and is fed and cared for by workers. Food is given to the larvae by trophallaxis, a process in which an ant regurgitates liquid food held in its crop. This is also how adults share food, stored in the "social stomach". Larvae, especially in the later stages, may also be provided solid food, such as trophic eggs, pieces of prey, and seeds brought by workers.



Meat eater ant nest during swarming

The larvae grow through a series of four or five moults and enter the pupal stage.

The pupa has the appendages free and not fused to the body as in a butterfly pupa.^[59] The differentiation into queens and workers (which are both female), and different castes of workers, is influenced in some species by the nutrition the larvae obtain. Genetic influences and the control of gene expression by the developmental environment are complex and the determination of caste continues to be a subject of research.^[60] Winged male ants, called drones, emerge from pupae along with the usually winged breeding females. Some species, such as army ants, have wingless queens. Larvae and pupae need to be kept at fairly constant temperatures to ensure proper development, and so often, are moved around among the various brood chambers within the colony.^[61]

A new ergate spends the first few days of its adult life caring for the queen and young. She then graduates to digging and other nest work, and later to defending the nest and foraging. These changes are sometimes fairly sudden, and define what are called temporal castes. An explanation for the sequence is suggested by the high casualties involved in foraging, making it an acceptable risk only for ants who are older and are likely to die soon of natural causes.^{[62][63]}

Ant colonies can be long-lived. The queens can live for up to 30 years, and workers live from 1 to 3 years. Males, however, are more transitory, being quite short-lived and surviving for only a few weeks.^[64] Ant queens are estimated to live 100 times as long as solitary insects of a similar size.^[65]

Ants are active all year long in the tropics, but, in cooler regions, they survive the winter in a state of dormancy known as hibernation. The forms of inactivity are varied and some temperate species have larvae going into the inactive state (diapause), while in others, the adults alone pass the winter in a state of reduced activity.^[66]

Reproduction

A wide range of reproductive strategies have been noted in ant species. Females of many species are known to be capable of reproducing asexually through thelytokous parthenogenesis.^[67] Secretions from the male accessory glands in some species can plug the female genital opening and prevent females from re-mating.^[68] Most ant species have a system in which only the queen and breeding females have the ability to mate. Contrary to popular belief, some ant nests have multiple queens, while others may exist without queens. Workers with the ability to reproduce are called "gamergates" and colonies that lack queens are then called gamergate colonies; colonies with queens are said to be queen-right.^[69]

Drones can also mate with existing queens by entering a foreign colony. When the drone is initially attacked by the workers, it releases a mating pheromone. If recognized as a mate, it will be carried to the queen to mate.^[70] Males may also patrol the nest and fight others by grabbing them with their mandibles, piercing their exoskeleton and then marking them with a pheromone. The marked male is interpreted as an invader by worker ants and is killed.^[71]



Fertilised meat-eater ant queen beginning to dig a new colony

Most ants are univoltine, producing a new generation each year.^[72] During the species-specific breeding period, winged females and

winged males, known to entomologists as alates, leave the colony in what is called a nuptial flight. The nuptial flight usually takes place in the late spring or early summer when the weather is hot and humid. Heat makes flying easier and freshly fallen rain makes the ground softer for mated queens to dig nests.^[73] Males typically take flight before the females. Males then use visual cues to find a common mating ground, for example, a landmark such as a pine tree to which

other males in the area converge. Males secrete a mating pheromone that females follow. Males will mount females in the air, but the actual mating process usually takes place on the ground. Females of some species mate with just one male but in others they may mate with as many as ten or more different males, storing the sperm in their spermathecae.^[74]

Mated females then seek a suitable place to begin a colony. There, they break off their wings and begin to lay and care for eggs. The females can selectively fertilise future eggs with the sperm stored to produce diploid workers or lay unfertilized haploid eggs to produce drones. The first workers to hatch are known as nanitics,^[75] and are weaker and smaller than later workers, but they begin to serve the colony immediately. They enlarge the nest, forage for food, and care for the other eggs. Species that have multiple queens may have a queen leaving the nest along with some workers to found a colony at a new site,^[74] a process akin to swarming in honeybees.



Alate male ant, *Prenolepis imparis*



Ants mating

Behaviour and ecology

Communication

Ants communicate with each other using pheromones, sounds, and touch.^[76] The use of pheromones as chemical signals is more developed in ants, such as the red harvester ant, than in other hymenopteran groups. Like other insects, ants perceive smells with their long, thin, and mobile antennae. The paired antennae provide information about the direction and intensity of scents. Since most ants live on the ground, they use the soil surface to leave pheromone trails that may be followed by other ants. In species that forage in groups, a forager that finds food marks a trail on the way back to the colony; this trail is followed by other ants, these ants then reinforce the trail when they head back with food to the colony. When the food source is exhausted, no new trails are marked by returning ants and the scent slowly dissipates. This behaviour helps ants deal with changes in their environment. For instance, when an established path to a food source is blocked by an obstacle, the foragers leave the path to explore new routes. If an ant is successful, it leaves a new trail marking the shortest route on its return. Successful trails are followed by more ants, reinforcing better routes and gradually identifying the best path.^[77]



Two *Camponotus sericeus* workers communicating through touch and pheromones

Ants use pheromones for more than just making trails. A crushed ant emits an alarm pheromone that sends nearby ants into an attack frenzy and attracts more ants from farther away. Several ant species even use "propaganda pheromones" to confuse enemy ants and make them fight among themselves.^[78] Pheromones are produced by a wide range of structures including Dufour's glands, poison glands and glands on the hindgut, pygidium, rectum, sternum, and hind tibia.^[65] Pheromones also are exchanged, mixed with food, and passed by trophallaxis, transferring information within the colony.^[79] This allows other ants to detect what task group (e.g., foraging or nest maintenance) other colony members belong to.^[80] In ant species with queen castes, when the dominant queen stops producing a specific pheromone, workers begin to raise new queens in the colony.^[81]

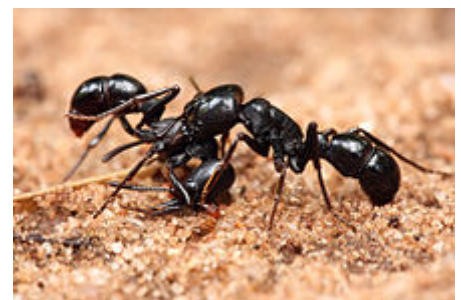
Some ants produce sounds by stridulation, using the gaster segments and their mandibles. Sounds may be used to communicate with colony members or with other species.^{[82][83]}

Defence

Ants attack and defend themselves by biting and, in many species, by stinging, often injecting or spraying chemicals, such as formic acid in the case of formicine ants, alkaloids and piperidines in fire ants, and a variety of protein components in other ants. Bullet ants (*Paraponera*), located in Central and South America, are considered to have the most painful sting of any insect, although it is usually not fatal to humans. This sting is given the highest rating on the Schmidt Sting Pain Index.

The sting of jack jumper ants can be fatal,^[84] and an antivenom has been developed for it.^[85]

Fire ants, *Solenopsis* spp., are unique in having a venom sac containing piperidine alkaloids.^[86] Their stings are painful and can be dangerous to hypersensitive people.^[87]



A *Plectroctena* sp. attacks another of its kind to protect its territory.



A weaver ant in fighting position, mandibles wide open

Trap-jaw ants of the genus *Odontomachus* are equipped with mandibles called trap-jaws, which snap shut faster than any other predatory appendages within the animal kingdom.^[88] One study of *Odontomachus bauri* recorded peak speeds of between 126 and 230 km/h (78 and 143 mph), with the jaws closing within 130 microseconds on average. The ants were also observed to use their jaws as a catapult to eject intruders or fling themselves backward to escape a threat.^[88] Before striking, the ant opens its mandibles extremely widely and locks them in this position by an internal mechanism. Energy is stored in a thick band of muscle and explosively released when triggered by the stimulation of sensory organs resembling hairs on the inside of the mandibles. The mandibles also permit slow and fine movements for other tasks. Trap-jaws also are seen in the

following genera: *Anochetus*, *Orectognathus*, and *Strumigenys*,^[88] plus some members of the Dacetini tribe,^[89] which are viewed as examples of convergent evolution.

A Malaysian species of ant in the *Camponotus cylindricus* group has enlarged mandibular glands that extend into their gaster. If combat takes a turn for the worse, a worker may perform a final act of suicidal altruism by rupturing the membrane of its gaster, causing the content of its mandibular glands to burst from the anterior region of its head, spraying a poisonous, corrosive secretion containing acetophenones and other chemicals that immobilise small insect attackers. The worker subsequently dies.^[90]

Suicidal defences by workers are also noted in a Brazilian ant, *Forelius pusillus*, where a small group of ants leaves the security of the nest after sealing the entrance from the outside each evening.^[91]

In addition to defence against predators, ants need to protect their colonies from pathogens. Some worker ants maintain the hygiene of the colony and their activities include undertaking or *necrophory*, the disposal of dead nest-mates.^[92] Oleic acid has been identified as the compound released from dead ants that triggers necrophoric behaviour in *Atta mexicana*^[93] while workers of *Linepithema humile* react to the absence of characteristic chemicals (dolichodial and iridomyrmecin) present on the cuticle of their living nestmates to trigger similar behaviour.^[94]

Nests may be protected from physical threats such as flooding and overheating by elaborate nest architecture.^{[95][96]} Workers of *Cataulacus muticus*, an arboreal species that lives in plant hollows, respond to flooding by drinking water inside the nest, and excreting it outside.^[97] *Camponotus anderseni*, which nests in the cavities of wood in mangrove habitats, deals with submergence under water by switching to anaerobic respiration.^[98]



Ant mound holes prevent water from entering the nest during rain.

Learning

Many animals can learn behaviours by imitation, but ants may be the only group apart from mammals where interactive teaching has been observed. A knowledgeable forager of *Temnothorax albipennis* will lead a naive nest-mate to newly discovered food by the process of tandem running. The follower obtains knowledge through its leading tutor. The leader is acutely sensitive to the progress of the follower and slows down when the follower lags and speeds up when the follower gets too close.^[99]

Controlled experiments with colonies of *Cerapachys biroi* suggest that an individual may choose nest roles based on her previous experience. An entire generation of identical workers was divided into two groups whose outcome in food foraging was controlled. One group was continually rewarded with prey, while it was made certain that the other failed. As a result, members of the successful group intensified their foraging attempts while the unsuccessful group ventured out fewer and fewer times. A month later, the successful foragers continued in their role while the others had moved to specialise in brood care.^[100]

Nest construction

Complex nests are built by many ant species, but other species are nomadic and do not build permanent structures. Ants may form subterranean nests or build them on trees. These nests may be found in the ground, under stones or logs, inside logs, hollow stems, or even acorns. The materials used for construction include soil and plant matter,^[74] and ants carefully select their nest sites; *Temnothorax albipennis* will avoid sites with dead ants, as these may indicate the presence of pests or disease. They are quick to abandon established nests at the first sign of threats.^[101]



Leaf nest of weaver ants, Pamalican, Philippines

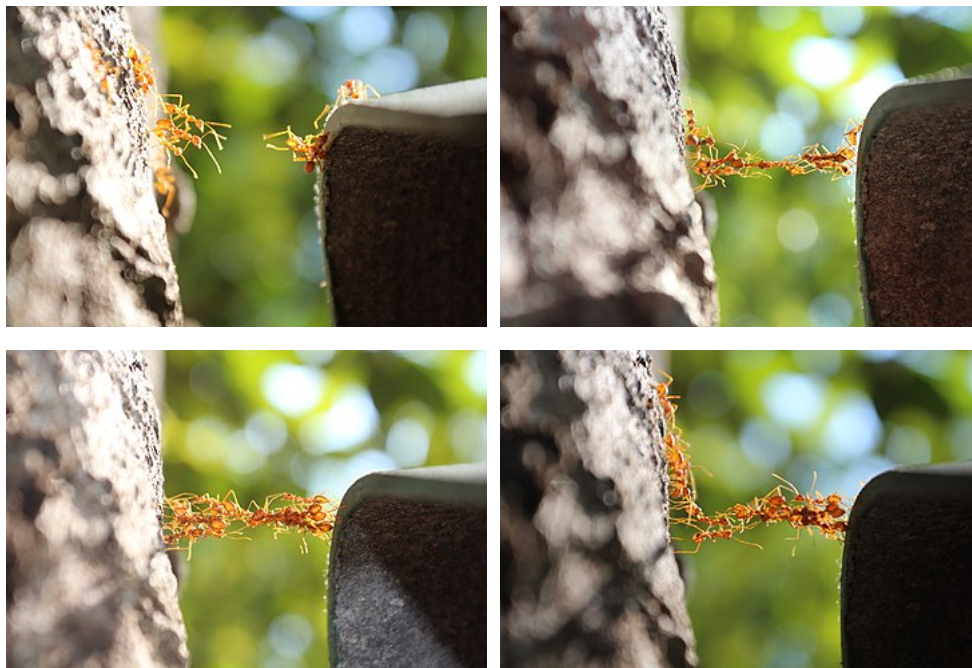
The army ants of South America, such as the *Eciton burchellii* species, and the driver ants of Africa do not build permanent nests, but instead, alternate between nomadism and stages where the workers form a temporary nest (bivouac) from their own bodies, by holding each other together.^[102]

Weaver ant (*Oecophylla* spp.) workers build nests in trees by attaching leaves together, first pulling them together with bridges of workers and then inducing their larvae to produce silk as they are moved along the leaf edges. Similar forms of nest construction are seen in some species of *Polyrhachis*.^[103]

Formica polycтена, among other ant species, constructs nests that maintain a relatively constant interior temperature that aids in the development of larvae. The ants maintain the nest temperature by choosing the location, nest materials, controlling ventilation and maintaining the heat from solar radiation, worker activity and metabolism, and in some moist nests, microbial activity in the nest materials.^[104]

Some ant species, such as those that use natural cavities, can be opportunistic and make use of the controlled micro-climate provided inside human dwellings and other artificial structures to house their colonies and nest structures.^{[105][106]}

Ant bridge



Cultivation of food



Myrmecocystus, honey pot ants, store food to prevent colony famine

Most ants are generalist predators, scavengers, and indirect herbivores,^[27] but a few have evolved specialised ways of obtaining nutrition. It is believed that many ant species that engage in indirect herbivory rely on specialized symbiosis with their gut microbes ^[107] to upgrade the nutritional value of the food they collect ^[108] and allow them to survive in nitrogen poor regions, such as rainforest canopies.^[109] Leafcutter ants (*Atta* and *Acromyrmex*) feed exclusively on a fungus that grows only within their colonies. They continually collect leaves which are taken to the colony, cut into tiny pieces and placed in fungal gardens. Ergates specialise in related tasks according to their sizes. The largest ants cut stalks, smaller workers chew the leaves and the smallest tend the fungus. Leafcutter ants are sensitive enough to recognise the reaction of the fungus to different plant material, apparently detecting chemical signals from the fungus.

If a particular type of leaf is found to be toxic to the fungus, the colony will no longer collect it. The ants feed on structures produced by the fungi called *gongylidia*. Symbiotic bacteria on the exterior surface of the ants produce antibiotics that kill bacteria introduced into the nest that may harm the fungi.^[110]

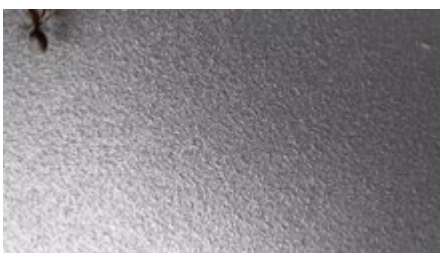
Navigation

Foraging ants travel distances of up to 200 metres (700 ft) from their nest ^[111] and scent trails allow them to find their way back even in the dark. In hot and arid regions, day-foraging ants face death by desiccation, so the ability to find the shortest route back to the nest reduces that risk. Diurnal desert ants of the genus *Cataglyphis* such as the Sahara desert ant navigate by keeping track of direction as well as distance travelled. Distances travelled are measured using an internal pedometer that keeps count of the steps taken^[112] and also by evaluating the movement of objects in their visual field (optical flow).^[113] Directions are measured using the position of the sun.^[114] They integrate this information to find the shortest route back to their nest.^[115] Like all ants, they can also make use of visual landmarks when available^[116] as well as olfactory and tactile cues to navigate.^{[117][118]} Some species of ant are able to use the Earth's magnetic field for navigation.^[119] The compound eyes of ants have specialised cells that detect polarised light from the Sun, which is used to determine direction.^{[120][121]} These polarization detectors are sensitive in the ultraviolet region of the light spectrum.^[122] In some army ant species, a group of foragers who become separated from the main column may sometimes turn back on themselves and form a circular ant mill. The workers may then run around continuously until they die of exhaustion.^[123]



An ant trail

Locomotion



Play media

Ant in Slow Motion

The female worker ants do not have wings and reproductive females lose their wings after their mating flights in order to begin their colonies. Therefore, unlike their wasp ancestors, most ants travel by walking. Some species are capable of leaping. For example, Jerdon's jumping ant (*Harpegnathos saltator*) is able to jump by synchronising the action of its mid and hind pairs of legs.^[124] There are several species of gliding ant including *Cephalotes atratus*; this may be a common trait among arboreal ants with small colonies. Ants with this ability are able to control their horizontal movement so as to catch tree trunks when they fall from atop the forest canopy.^[125]

Other species of ants can form chains to bridge gaps over water, underground, or through spaces in vegetation. Some species also form floating rafts that help them survive floods.^[126] These rafts may also have a role in allowing ants to colonise islands.^[127] *Polyrhachis sokolova*, a species of ant found in Australian mangrove swamps, can swim and live in underwater nests. Since they lack gills, they go to trapped pockets of air in the submerged nests to breathe.^[128]

Cooperation and competition

Not all ants have the same kind of societies. The Australian bulldog ants are among the biggest and most basal of ants. Like virtually all ants, they are eusocial, but their social behaviour is poorly developed compared to other species. Each individual hunts alone, using her large eyes instead of chemical senses to find prey.^[129]

Some species (such as *Tetramorium caespitum*) attack and take over neighbouring ant colonies. Others are less expansionist, but just as aggressive; they invade colonies to steal eggs or larvae, which they either eat or raise as workers or slaves. Extreme specialists among these slave-raiding ants, such as the Amazon ants, are incapable of feeding themselves and need captured workers to survive.^[130] Captured workers of enslaved *Temnothorax* species have evolved a counter strategy, destroying just the female pupae of the slave-making *Temnothorax americanus*, but sparing the males (who don't take part in slave-raiding as adults).^[131]



Meat-eater ants feeding on a cicada: social ants cooperate and collectively gather food



A worker *Harpegnathos saltator* (a jumping ant) engaged in battle with a rival colony's queen

Ants identify kin and nestmates through their scent, which comes from hydrocarbon-laced secretions that coat their exoskeletons. If an ant is separated from its original colony, it will eventually lose the colony scent. Any ant that enters a colony without a matching scent will be attacked.^[132] Also, the reason why two separate colonies of ants will attack each other even if they are of the same species is because the genes responsible for pheromone production are different between them. The Argentine ant, however, does not have this characteristic, due to lack of genetic diversity, and has become a global pest because of it.

Parasitic ant species enter the colonies of host ants and establish themselves as social parasites; species such as *Strumigenys xenos* are entirely parasitic and do not have workers, but instead, rely on the food gathered by their *Strumigenys perplexa* hosts.^{[133][134]} This form of parasitism is seen across many ant genera, but the parasitic ant is usually a species that is closely related to its host. A variety of methods are employed to enter the nest of the host ant. A parasitic queen may enter the host nest before the first brood has hatched, establishing herself prior to development of a colony scent. Other species use pheromones to confuse the host ants or to trick them into carrying the parasitic queen into the nest. Some simply fight their way into the nest.^[135]

A conflict between the sexes of a species is seen in some species of ants with these reproducers apparently competing to produce offspring that are as closely related to them as possible. The most extreme form involves the production of clonal offspring. An extreme of sexual conflict is seen in *Wasmannia auropunctata*, where the queens produce diploid daughters by thelytokous parthenogenesis and males produce clones by a process whereby a diploid egg loses its maternal contribution to produce haploid males who are clones of the father.^[136]

Relationships with other organisms

Ants form symbiotic associations with a range of species, including other ant species, other insects, plants, and fungi. They also are preyed on by many animals and even certain fungi. Some arthropod species spend part of their lives within ant nests, either preying on ants, their larvae, and eggs, consuming the food stores of the ants, or avoiding predators. These inquilines may bear a close resemblance to ants. The nature of this ant mimicry (myrmecomorphy) varies, with some cases involving Batesian mimicry, where the mimic reduces the risk of predation. Others show Wasmannian mimicry, a form of mimicry seen only in inquilines.^{[137][138]}



The spider *Myrmarachne plataleoides* (female shown) mimics weaver ants to avoid predators.



An ant collects honeydew from an aphid

Aphids and other hemipteran insects secrete a sweet liquid called honeydew, when they

feed on plant sap. The sugars in honeydew are a high-energy food source, which many ant species collect.^[139] In some cases, the aphids secrete the honeydew in response to ants tapping them with their antennae. The ants in turn keep predators away from the aphids and will move them from one feeding location to another. When migrating to a new area, many colonies will take the aphids with them, to ensure a continued supply of honeydew. Ants also tend mealybugs to harvest their honeydew. Mealybugs may become a serious pest of pineapples if ants are present to protect mealybugs from their natural enemies.^[140]

Myrmecophilous (ant-loving) caterpillars of the butterfly family Lycaenidae (e.g., blues, coppers, or hairstreaks) are herded by the ants, led to feeding areas in the daytime, and brought inside the ants' nest at night. The caterpillars have a gland which secretes honeydew when the ants massage them. Some caterpillars produce vibrations and sounds that are perceived by the ants.^[141] A similar adaptation can be seen in Grizzled skipper butterflies that emit vibrations by expanding their wings in order to communicate with ants, which are natural predators of these butterflies.^[142] Other caterpillars have evolved from ant-loving to ant-eating: these myrmecophagous caterpillars secrete a pheromone that makes the ants act as if the caterpillar is one of their own larvae. The caterpillar is then taken into the ant nest where it feeds on the ant larvae.^[143] A number of specialized bacteria have been found as endosymbionts in ant guts. Some of the dominant bacteria belong to the order Rhizobiales whose members are known for being nitrogen-fixing symbionts in legumes but the species found in ant lack the ability to fix nitrogen.^{[144][145]} Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus in the genera *Leucoagaricus* or *Leucocoprinus* of the family Agaricaceae. In this ant-fungus mutualism, both species depend on each other for survival. The ant *Allomerus decemarticulatus* has evolved a three-way association with the host plant, *Hirtella physophora* (Chrysobalanaceae), and a sticky fungus which is used to trap their insect prey.^[146]

Lemon ants make devil's gardens by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees, (*Duroia hirsuta*). This modification of the forest provides the ants with more nesting sites inside the stems of the *Duroia* trees.^[147] Although some ants obtain nectar from flowers, pollination by ants is somewhat rare, one example being of the pollination of the orchid *Leporella fimbriata* which induces male *Myrmecia urens* to pseudocopulate with the flowers, transferring pollen in the process.^[148] One theory that has been proposed for the rarity of pollination is that the secretions of the metapleural gland inactivate and reduce the viability of pollen.^{[149][150]} Some plants have special nectar exuding structures, extrafloral nectaries, that provide food for ants, which in turn protect the plant from more damaging herbivorous insects.^[151] Species such as the bullhorn acacia (*Acacia cornigera*) in Central America have



Ants may obtain nectar from flowers such as the dandelion but are only rarely known to pollinate flowers.

hollow thorns that house colonies of stinging ants (*Pseudomyrmex ferruginea*) who defend the tree against insects, browsing mammals, and epiphytic vines. Isotopic labelling studies suggest that plants also obtain nitrogen from the ants.^[152] In return, the ants obtain food from protein- and lipid-rich Beltian bodies. In Fiji *Philidris nagasau* (Dolichoderinae) are known to selectively grow species of epiphytic *Squamellaria* (Rubiaceae) which produce large domatia inside which the ant colonies nest. The ants plant the seeds and the domatia of young seedling are immediately occupied and the ant faeces in them contribute to rapid growth.^[153] Similar dispersal associations are found with other dolichoderines in the region as well.^[154] Another example of this type of ectosymbiosis comes from the *Macaranga* tree, which has stems adapted to house colonies of *Crematogaster* ants.^[155]

Many plant species have seeds that are adapted for dispersal by ants.^[156] Seed dispersal by ants or myrmecochory is widespread, and new estimates suggest that nearly 9% of all plant species may have such ant associations.^{[157][156]} Often, seed-dispersing ants perform directed dispersal, depositing the seeds in locations that increase the likelihood of seed survival to reproduction.^[158] Some plants in arid, fire-prone systems are particularly dependent on ants for their survival and dispersal as the seeds are transported to safety below the ground.^[159] Many ant-dispersed seeds have special external structures, elaiosomes, that are sought after by ants as food.^[160]

A convergence, possibly a form of mimicry, is seen in the eggs of stick insects. They have an edible elaiosome-like structure and are taken into the ant nest where the young hatch.^[161]



A meat ant tending a common leafhopper nymph

Most ants are predatory and some prey on and obtain food from other social insects including other ants. Some species specialise in preying on termites (*Megaponera* and *Termitopone*) while a few Cerapachyinae prey on other ants.^[111] Some termites, including *Nasutitermes corniger*, form associations with certain ant species to keep away predatory ant species.^[162] The tropical wasp *Mischocyttarus drewseni* coats the pedicel of its nest with an ant-repellent chemical.^[163] It is suggested that many tropical wasps may build their nests in trees and cover them to protect themselves from ants. Other wasps, such as *A. multipicta*, defend against ants by blasting them off the nest with bursts of wing buzzing.^[164] Stingless bees (*Trigona* and *Melipona*) use chemical defences against ants.^[111]

Flies in the Old World genus *Bengalia* (Calliphoridae) prey on ants and are kleptoparasites, snatching prey or brood from the mandibles of adult ants.^[165] Wingless and legless females of the Malaysian phorid fly (*Vestigipoda myrmolarvoidea*) live in the nests of ants of the genus *Aenictus* and are cared for by the ants.^[165]

Fungi in the genera *Cordyceps* and *Ophiocordyceps* infect ants. Ants react to their infection by climbing up plants and sinking their mandibles into plant tissue. The fungus kills the ants, grows on their remains, and produces a fruiting body. It appears that the fungus alters the behaviour of the ant to help disperse its spores^[166] in a microhabitat that best suits the fungus.^[167] Strepsipteran parasites also manipulate their ant host to climb grass stems, to help the parasite find mates.^[168]

A nematode (*Myrmeconema neotropicum*) that infects canopy ants (*Cephalotes atratus*) causes the black-coloured gasters of workers to turn red. The parasite also alters the behaviour of the ant, causing them to carry their gasters high. The conspicuous red gasters are mistaken by birds for ripe fruits, such as *Hyeronima alchorneoides*, and eaten. The droppings of the bird are collected by other ants and fed to their young, leading to further spread of the nematode.^[169]

South American poison dart frogs in the genus *Dendrobates* feed mainly on ants, and the toxins in their skin may come from the ants.^[170]

Army ants forage in a wide roving column, attacking any animals in that path that are unable to escape. In Central and South America, *Eciton burchellii* is the swarming ant most commonly attended by "ant-following" birds such as antbirds and woodcreepers.^{[171][172]} This behaviour was once considered mutualistic, but later studies found the birds to be parasitic. Direct

kleptoparasitism (birds stealing food from the ants' grasp) is rare and has been noted in Inca doves which pick seeds at nest entrances as they are being transported by species of *Pogonomyrmex*.^[173] Birds that follow ants eat many prey insects and thus decrease the foraging success of ants.^[174] Birds indulge in a peculiar behaviour called anting that, as yet, is not fully understood. Here birds rest on ant nests, or pick and drop ants onto their wings and feathers; this may be a means to remove ectoparasites from the birds.



Spiders sometimes feed on ants.

Anteaters, armadillos, pangolins, echidnas and numbats have special adaptations for living on a diet of ants. These adaptations include long, sticky tongues to capture ants and strong claws to break into ant nests. Brown bears (*Ursus arctos*) have been found to feed on ants. About 12%, 16%, and 4% of their faecal volume in spring, summer, and autumn, respectively, is composed of ants.^[175]

Relationship with humans

Ants perform many ecological roles that are beneficial to humans, including the suppression of pest populations and aeration of the soil. The use of weaver ants in citrus cultivation in southern China is considered one of the oldest known applications of biological control.^[14] On the other hand, ants may become nuisances when they invade buildings, or cause economic losses.

In some parts of the world (mainly Africa and South America), large ants, especially army ants, are used as surgical sutures. The wound is pressed together and ants are applied along it. The ant seizes the edges of the wound in its mandibles and locks in place. The body is then cut off and the head and mandibles remain in place to close the wound.^{[176][177][178]} The large heads of the dinergates (soldiers) of the leafcutting ant *Atta cephalotes* are also used by native surgeons in closing wounds.^[179]

Some ants have toxic venom and are of medical importance. The species include *Paraponera clavata* (tocandira) and *Dinoponera* spp. (false tocandiras) of South America^[180] and the *Myrmecia* ants of Australia.^[181]

In South Africa, ants are used to help harvest the seeds of rooibos (*Aspalathus linearis*), a plant used to make a herbal tea. The plant disperses its seeds widely, making manual collection difficult. Black ants collect and store these and other seeds in their nest, where humans can gather them *en masse*. Up to half a pound (200 g) of seeds may be collected from one ant-heap.^{[182][183]}

Although most ants survive attempts by humans to eradicate them, a few are highly endangered. These tend to be island species that have evolved specialized traits and risk being displaced by introduced ant species. Examples include the critically endangered Sri Lankan relict ant (*Aneuretus simoni*) and *Adetomyrma venatrix* of Madagascar.^[184]

It has been estimated by E.O. Wilson that the total number of individual ants alive in the world at any one time is between one and ten quadrillion (short scale) (i.e., between 10^{15} and 10^{16}). According to this estimate, the total biomass of all the ants in the world is approximately equal to the total biomass of the entire human race.^[185] Also, according to this estimate, there are approximately 1 million ants for every human on Earth.^[186]

As food



Weaver ants are used as a biological control for citrus cultivation in southern China.



Roasted ants in Colombia



Ant larvae for sale in Isaan, Thailand

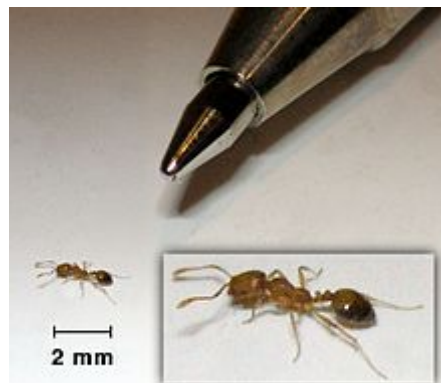
Ants and their larvae are eaten in different parts of the world. The eggs of two species of ants are used in Mexican *escamoles*. They are considered a form of insect caviar and can sell for as much as US\$40 per pound (\$90/kg) because they are seasonal and hard to find. In the Colombian department of Santander, *hormigas culonas* (roughly interpreted as "large-bottomed ants") *Atta laevigata* are toasted alive and eaten.^[187]

In areas of India, and throughout Burma and Thailand, a paste of the green weaver ant (*Oecophylla smaragdina*) is served as a condiment with curry.^[188] Weaver ant eggs and larvae, as well as the ants, may be used in a Thai salad, *yam* (Thai: ยำ), in a dish called *yam khai mot daeng* (Thai: ยำไข่มดแดง) or red ant egg salad, a dish that comes from the Issan or north-eastern region of Thailand. Saville-Kent, in the *Naturalist in Australia* wrote "Beauty, in the case of the green ant, is more than skin-deep. Their attractive, almost sweetmeat-like translucency possibly invited the first essays at their consumption by the human species". Mashed up in water, after the manner of lemon squash, "these ants form a pleasant acid drink which is held in high favor by the natives of North Queensland, and is even appreciated by many European palates".^[189]

In his *First Summer in the Sierra*, John Muir notes that the Digger Indians of California ate the tickling, acid gasters of the large jet-black carpenter ants. The Mexican Indians eat the replete workers, or living honey-pots, of the honey ant (*Myrmecocystus*).^[189]

As pests

Some ant species are considered as pests, primarily those that occur in human habitations, where their presence is often problematic. For example, the presence of ants would be undesirable in sterile places such as hospitals or kitchens. Some species or genera commonly categorized as pests include the Argentine ant, pavement ant, yellow crazy ant, banded sugar ant, pharaoh ant, carpenter ants, odorous house ant, red imported fire ant, and European fire ant. Some ants will raid stored food, others may damage indoor structures, some can damage agricultural crops directly (or by aiding sucking pests), and some will sting or bite.^[15] The adaptive nature of ant colonies make it nearly impossible to eliminate entire colonies and most pest management practices aim to control local populations and tend to be temporary solutions. Ant populations are managed by a combination of approaches that make use of chemical, biological and physical methods. Chemical methods include the use of insecticidal bait which is gathered by ants as food and brought back to the nest where the poison is inadvertently spread to other colony members through trophallaxis. Management is based on the species and techniques can vary according to the location and circumstance.^[15]



The tiny pharaoh ant is a major pest in hospitals and office blocks; it can make nests between sheets of paper.

In science and technology

Observed by humans since the dawn of history, the behaviour of ants has been documented and the subject of early writings and fables passed from one century to another. Those using scientific methods, myrmecologists, study ants in the laboratory and in their natural conditions. Their complex and variable social structures have made ants ideal model organisms. Ultraviolet vision

was first discovered in ants by Sir John Lubbock in 1881.^[190] Studies on ants have tested hypotheses in ecology and sociobiology, and have been particularly important in examining the predictions of theories of kin selection and evolutionarily stable strategies.^[191] Ant colonies may be studied by rearing or temporarily maintaining them in *formicaria*, specially constructed glass framed enclosures.^[192] Individuals may be tracked for study by marking them with dots of colours.^[193]

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems, for example Ant colony optimization and Ant robotics. This area of biomimetics has led to studies of ant locomotion, search engines that make use of "foraging trails", fault-tolerant storage, and networking algorithms.^[13]



Camponotus nearcticus workers travelling between two formicaria through connector tubing

As pets

From the late 1950s through the late 1970s, ant farms were popular educational children's toys in the United States. Some later commercial versions use transparent gel instead of soil, allowing greater visibility at the cost of stressing the ants with unnatural light.^[194]

In culture



Aesop's ants: picture by Milo Winter, 1888–1956

Anthropomorphised ants have often been used in fables and children's stories to represent industriousness and cooperative effort. They also are mentioned in religious texts.^{[195][196]} In the Book of Proverbs in the Bible, ants are held up as a good example for humans for their hard work and cooperation.^[197] Aesop did the same in his fable The Ant and the Grasshopper. In the Quran, Sulayman is said to have heard and understood an ant warning other ants to return home to avoid being accidentally crushed by Sulayman and his marching army. [Quran 27:18 (<http://www.perseus.tufts.edu/hopper/text?doc=Perseus%3Atext%3A2002.02.0006%3Aasura%3D27%3Averse%3D18>)]^[198] In parts of Africa, ants are considered to be the messengers of the deities. Some Native American mythology, such as the Hopi mythology, considers ants as the very first animals. Ant bites are often said to have curative properties. The sting of some species of *Pseudomyrmex* is claimed to give fever relief.^[199] Ant bites are used in the initiation ceremonies of some Amazon Indian cultures as a test of endurance.^{[200][201]}

Ant society has always fascinated humans and has been written about both humorously and seriously. Mark Twain wrote about ants in his 1880 book *A Tramp Abroad*.^[202] Some modern authors have used the example of the ants to comment on the relationship between society and the individual. Examples are Robert Frost in his poem "Departmental" and T. H. White in his fantasy novel *The Once and Future King*. The plot in French entomologist and writer Bernard Werber's *Les Fourmis* science-fiction trilogy is divided between the worlds of ants and humans; ants and their behaviour is described using contemporary scientific knowledge. H.G. Wells wrote about intelligent ants destroying human settlements in Brazil and threatening human civilization in his 1905 science-fiction short story, *The Empire of the Ants*. In more recent times, animated cartoons and 3-D animated films featuring ants have been produced including *Antz*, *A Bug's Life*, *The Ant Bully*, *The Ant and the Aardvark*, *Ferdie the Ant* and *Atom Ant*. Renowned myrmecologist E. O. Wilson wrote a short story, "Trailhead" in 2010 for *The New Yorker*

magazine, which describes the life and death of an ant-queen and the rise and fall of her colony, from an ants' point of view.^[203] The French neuroanatomist, psychiatrist and eugenicist Auguste Forel believed that ant societies were models for human society. He published a five volume work from 1921 to 1923 that examined ant biology and society.^[204]

In the early 1990s, the video game *SimAnt*, which simulated an ant colony, won the 1992 Codie award for "Best Simulation Program".^[205]

Ants also are quite popular inspiration for many science-fiction insectoids, such as the Formics of *Ender's Game*, the Bugs of *Starship Troopers*, the giant ants in the films *Them!* and *Empire of the Ants*, Marvel Comics' super hero Ant-Man, and ants mutated into super-intelligence in *Phase IV*. In computer strategy games, ant-based species often benefit from increased production rates due to their single-minded focus, such as the Klackons in the *Master of Orion* series of games or the ChCht in *Deadlock II*. These characters are often credited with a hive mind, a common misconception about ant colonies.^[206]

See also

- Ant robotics
- Ant venom
- Glossary of ant terms
- International Union for the Study of Social Insects
- *Myrmecological News* (journal)
- Task allocation and partitioning of social insects

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House dust mite

House dust mites (**HDM**, or simply **dust mites**) are mites found in association with dust in dwellings.^[1]

The main species are:

- *Dermatophagoides farinae* (American house dust mite)
- *Dermatophagoides microceras*
- *Dermatophagoides pteronyssinus* (European house dust mite)
- *Euroglyphus maynei* (Mayne's house dust mite)



House dust mites
(*Dermatophagoides pteronyssinus*)
aggregate

Contents

Biology

- Taxonomy
- Characteristics
- Diet
- Predators
- Reproduction
- Distribution

Health issues

- Allergies
- Oral mite anaphylaxis

Control techniques

- Furniture
- Bed linen
- Indoor climate

See also

References

External links

Biology

Taxonomy

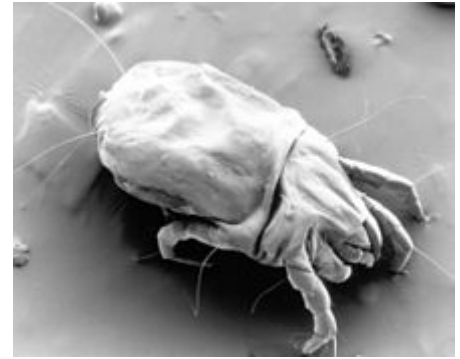
The dust mites are cosmopolitan members of the mite family Pyroglyphidae.

Characteristics

House dust mites, due to their very small size and translucent bodies, are barely visible to the unaided eye.^[2] A typical house dust mite measures 0.2–0.3 mm (0.008–0.012 in) in length.^[3] For accurate identification, one needs at least 10× magnification. The body of the house dust mite has a striated cuticle.

Diet

They feed on skin flakes from animals, including humans, and on some mold. *Dermatophagoides farinae* fungal food choices in 16 tested species commonly found in homes was observed *in vitro* to be *Alternaria alternata*, *Cladosporium sphaerospermum*, and *Wallemia sebi*, and they disliked *Penicillium chrysogenum*, *Aspergillus versicolor*, and *Stachybotrys chartarum*.^[4]



A scanning electron micrograph of a female dust mite

Predators

The predators of dust mites are other allergenic mites (*Cheyletiella*), silverfish and pseudoscorpions.^[5]

Reproduction

The average life cycle for a house dust mite is 65–100 days.^[6] A mated female house dust mite can live up to 70 days, laying 60 to 100 eggs in the last five weeks of her life. In a 10-week life span, a house dust mite will produce approximately 2,000 fecal particles and an even larger number of partially digested enzyme-covered dust particles.

Distribution

Dust mites are found worldwide, but are found more commonly in humid regions.^[7] The species *Blomia tropicalis* is typically found only in tropical or subtropical regions.^[8] Detectable dust mite allergen was found in the beds of about 84% of surveyed United States homes.^[9] In Europe, detectable Der p 1 or Der f 1 allergen was found in 68% of surveyed homes.^[10]

Health issues

Allergies

The mite's gut contains potent digestive enzymes (notably Peptidase 1) that persist in their feces and are major inducers of allergic reactions such as wheezing. The mite's exoskeleton can also contribute to allergic reactions. Unlike scabies mites or skin follicle mites, house dust mites do not burrow under the skin and are not parasitic.^[11]

Severe dust mite infestation in the home has been linked to atopic dermatitis and epidermal barrier damage has been documented.^[12]

House dust mites are associated with allergic rhinitis and asthma,^[13] as well as allergic conjunctivitis.^[14] Efforts to remove these mites from the environment have not been found to be effective.^[13] Immunotherapy may be useful in those affected.^[13] Subcutaneous injections have better evidence than under the tongue dosing.^[15] Topical steroids as nasal spray or inhalation may be used.^[16]

Oral mite anaphylaxis

Dermatophagoides spp. can cause oral mite anaphylaxis (AKA pancake syndrome) when found in flour.^{[17][18]}

Control techniques

House dust mites are present indoors wherever humans live. Positive tests for dust mite allergies are extremely common among people with asthma. Dust mites are microscopic arachnids whose primary food is dead human skin cells, but they do not live on living people. They and their feces and other allergens which they produce are major constituents of house dust, but because they are so heavy they are not suspended for long in the air. They are generally found on the floor and other surfaces until disturbed (by walking, for example). It could take somewhere between twenty minutes and two hours for dust mites to settle back down out of the air.

Dust mites are a nesting species that prefers a dark, warm, and humid climate. They flourish in mattresses, bedding, upholstered furniture, and carpets. Their feces include enzymes that are released upon contact with a moist surface, which can happen when a person inhales, and these enzymes can kill cells within the human body.^[19] House dust mites did not become a problem until humans began to use textiles, such as western style blankets and clothing.^[20]

Furniture

Furniture with wooden or leather surfaces reduce the dust mite population.^[21]

Bed linen

Hot tumble drying a bed linen for 1 hour will kill 99% of mites therein.^[22]

Weekly changing the bed linen reduces the risk of exposure to dust mites.^[16]

Cotton covers not covered with complete mattress covers are very likely to become colonised by bacteria and molds; they must be cleaned periodically (at least every second to third month).^[23]

Dust mite eggs are freeze tolerant (-70°C for 30 minutes); hatching can normally be prevented by exposure of fabrics to:^[24]

- Direct sunlight for 3 hours or
- Dry or wet heat of at least 60°C (140°F) for a minimum of 30 minutes.

Dust mites drown in water.^[25]

Good properties of anti-mite fabrics have been identified as being:^[26]

- Thread count greater than 246.
- Pore size of between 2 and 10 microns.
- Allergen impenetrability $>99\%$.
- Dust leakage of less than 4%.
- Breathability between 2 and $6\text{ cm}^3/\text{second}/\text{cm}^2$.

Indoor climate

Allergy patients are advised to keep the relative humidity below 50%, if possible. Very few mites can survive if the humidity is less than 45% (at 22°C (72°F)). However, they can survive if the humidity is high just for an hour and a half per day, for example due to cooking.^[25]



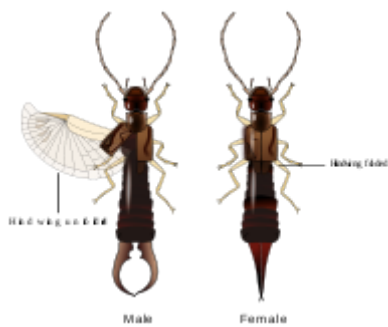
Dust mite-proof encasements to mattress, pillow, and duvet, prevents chronic contact with allergens.^{[16][21]}

Contents

Earwig											
Temporal range: 208–0 Ma											
PreЄ	Є	OS	D	C	P	T	J	K	PgN		
Late Triassic to Recent											
											
Female common earwig, <i>Forficula auricularia</i>											
Scientific classification 											
Kingdom:		Animalia									
Phylum:		Arthropoda									
Class:		Insecta									
Infraclass:		Neoptera									
Superorder:		Exopterygota									
Order:		Dermaptera De Geer, 1773									
Suborders											
<ul style="list-style-type: none"> †Archidermaptera †Eodermaptera Neodermaptera 											
Synonyms											
<ul style="list-style-type: none"> Euplecoptera Euplexoptera Forficulida 											

Etymology

The scientific name for the order, "Dermaptera", is Greek in origin, stemming from the words *derma*, meaning skin, and *pteron* (plural *ptera*), wing. It was coined by Charles De Geer in 1773. The common term, *earwig*, is derived from the Old English *ēare*, which means "ear", and *wicga*, which means "insect", or literally, "beetle".^[2] Entomologists suggest that the origin of the name is a reference to the appearance of the hindwings, which are unique and distinctive among insects, and resemble a human ear when unfolded.^{[3][4]} The name is more popularly thought to be related to the old wives' tale that earwigs burrowed into the brains of humans through the ear and laid their eggs there.^[5] Earwigs are not known to purposefully climb into ear canals, but there have been anecdotal reports of earwigs being found in the ear.^[6]



Earwig diagram with wings extended and closed

Distribution

Earwigs are abundant and can be found throughout the Americas and Eurasia. The common earwig was introduced into North America in 1907 from Europe, but tends to be more common in the southern and southwestern parts of the United States.^{[7]:739} The only native species of earwig found in the north of the United States is the spine-tailed earwig (*Doru aculeatum*),^{[8]:144} found as far north as Canada, where it hides in the leaf axils of emerging plants in southern Ontario wetlands. However, other families can be found in North America, including Forficulidae (*Doru* and *Forficula* being found there), Spongiphoridae, Anisolabididae, and Labiduridae.^[9]

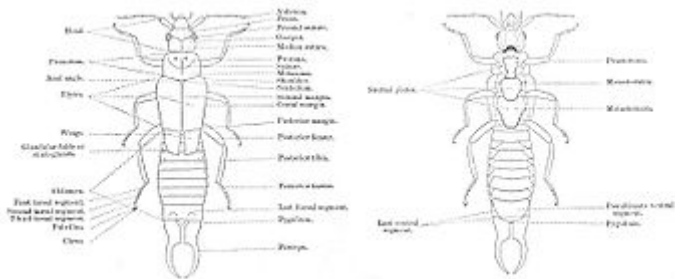


An earwig from the Western Ghats

Few earwigs survive winter outdoors in cold climates. They can be found in tight crevices in woodland, fields and gardens.^{[7]:739[10]} Out of about 1,800 species, about 25 occur in North America, 45 in Europe (including 7 in Great Britain), and 60 in Australia.^[11]

Morphology

Most earwigs are flattened (which allows them to fit inside tight crevices, such as under bark) with an elongated body generally 7–50 millimetres (0.28–1.97 in) long.^[11] The largest extant species is the Australian giant earwig (*Titanolabis colosseus*) which is approximately 50 mm (2.0 in) long,^{[12]:10} while the possibly extinct Saint Helena earwig (*Labidura herculeana*) reached 78 mm (3.1 in).^[13] Earwigs are characterized by the cerci, or the pair of forceps-like pincers on their abdomen; male earwigs generally have more curved pincers than females. These pincers are used to capture prey, defend themselves and fold their wings under the short tegmina.^[14] The antennae are thread-like with at least 10 segments.^{[7]:738–739}



Male earwig, external morphology. Click on image for a larger view

^[14] The antennae are thread-like with at least 10 segments.^{[7]:738–739}

The forewings are short oblong leathery plates used to cover the hindwings like the elytra of a beetle, rather than to fly. Most species have short and leather-like forewings with very thin hindwings, though species in the former suborders Arixeniina and Hemimerina (epizoic species, sometimes considered as ectoparasites^{[15][16]}) are wingless and blind with filiform segmented cerci (today these are both included merely as families in the suborder Neodermaptera).^{[11][17][18]} The hindwing is a very thin membrane that expands like a fan, radiating from one point folded under the forewing. Even though most earwigs have wings and are capable of flight, they are rarely seen in flight. These wings are unique in venation and in the pattern of folding that requires the use of the cerci.^[19]

Internal

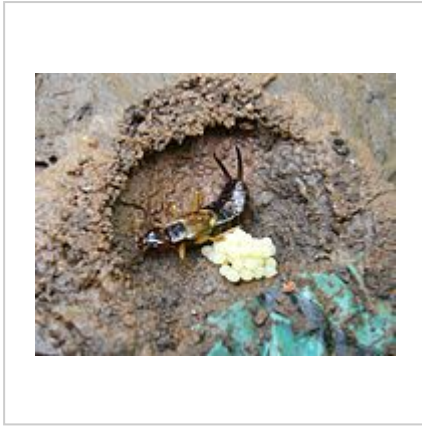
The neuroendocrine system is typical of insects. There is a brain, a subesophageal ganglion, three thoracic ganglia, and six abdominal ganglia. Strong neuron connections connect the neurohemal corpora cardiaca to the brain and frontal ganglion, where the closely related median corpus allatum produces juvenile hormone III in close proximity to the neurohemal dorsal aorta. The digestive system of earwigs is like all other insects, consisting of a fore-, mid-, and hindgut, but earwigs lack gastric caecae which are specialized for digestion in many species of insect. Long, slender (excretory) malpighian tubules can be found between the junction of the mid- and hind gut.^[20]

The reproductive system of females consist of paired ovaries, lateral oviducts, spermatheca, and a genital chamber. The lateral ducts are where the eggs leave the body, while the spermatheca is where sperm is stored. Unlike other insects, the gonopore, or genital opening is behind the seventh abdominal segment. The ovaries are primitive in that they are polytrophic (the nurse cells and oocytes alternate along the length of the ovariole). In some species these long ovarioles branch off the lateral duct, while in others, short ovarioles appear around the duct.^[20]

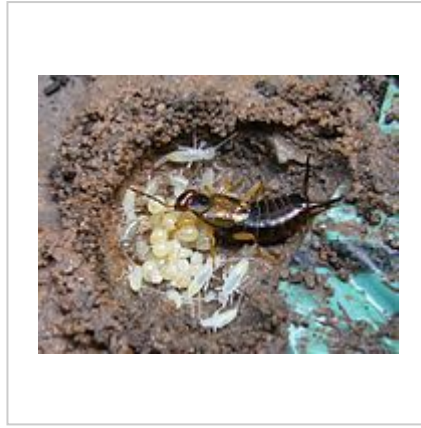
Life cycle and reproduction

Earwigs are hemimetabolous, meaning they undergo incomplete metamorphosis, developing through a series of 4 to 6 molts. The developmental stages between molts are called instars. Earwigs live for about a year from hatching. They start mating in the autumn, and can be found together in the autumn and winter. The male and female will live in a chamber in debris, crevices, or soil 2.5 centimetres (1 in) deep.^{[7]:739} After mating, the sperm may remain in the female for months before the eggs are fertilized. From midwinter to early spring, the male will leave, or be driven out by the female. Afterward the female will begin to lay 20 to 80 pearly white eggs in 2 days. Some earwigs, those parasitic in the suborders Arixeniina and Hemimerina, are viviparous (give birth to live young); they would be fed by a sort of placenta.^{[7]:739–740[17]} When first laid, the eggs are white or cream-colored and oval-shaped, but right before hatching they become kidney-shaped and brown.^[21] Each egg is approximately 1 mm (0.04 in) tall and 0.8 mm (0.03 in) wide.^[18]

Earwigs are among the few non-social insect species that show maternal care. The mother will pay close attention to the needs of her eggs, such as warmth and protection, though studies have shown that the mother does not pay attention to the eggs as she collects them.^[17] The mother has been shown to pick up wax balls by accident, but they would eventually be rejected as they do not have the proper scent. The mother will also faithfully defend the eggs from predators, not leaving them to eat unless the clutch goes bad.^{[7]:740} Another distinct maternal care unique to earwigs is that the mother continuously cleans the eggs to protect them from fungi. Studies have found that the urge to clean the eggs persists for days after they are removed; when the eggs were replaced after hatching, the mother continued to clean them for up to 3 months.^[17]

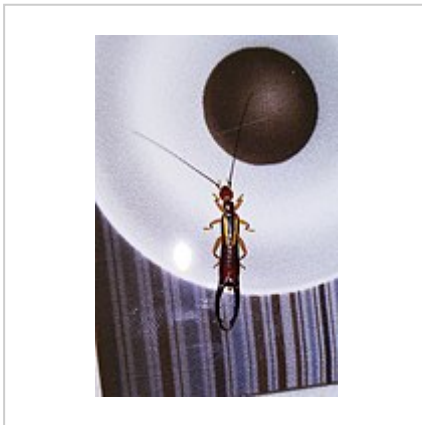


Female earwig in her nest, with eggs

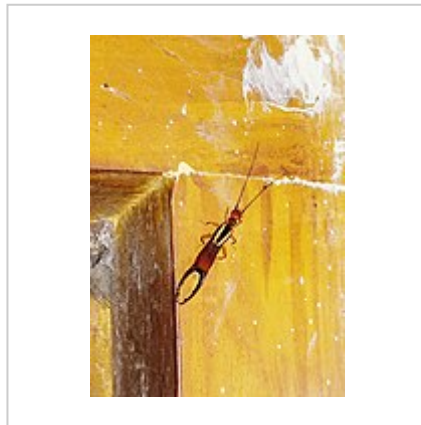


Female earwig in her nest with newly hatched young

The eggs hatch in about 7 days. The mother may assist the nymphs in hatching. When the nymphs hatch, they eat the egg casing and continue to live with the mother. The nymphs look similar to their parents, only smaller, and will nest under their mother and she will continue to protect them until their second molt. The nymphs feed on food regurgitated by the mother,^[22] and on their own molts. If the mother dies before the nymphs are ready to leave, the nymphs may eat her.^{[7]:740[23]}



An earwig on a wall in Haldia, West Bengal, India.



An earwig on a wooden door in Haldia, West Bengal, India.

Earwig life cycle



The life cycle and development of a male earwig from egg to each instar

After five to six instars, the nymphs will molt into adults. The male's forceps will become curved, while the females' forceps remain straight. They will also develop their natural color, which can be anything from a light brown (as in the Tawny earwig) to a dark black (as in the Ringlegged earwig). In species of winged earwigs, the wings will start to develop at this time. The forewings of an earwig are sclerotized to serve as protection for the membranous hindwings.

Behavior

Most earwigs are nocturnal and inhabit small crevices, living in small amounts of debris, in various forms such as bark and fallen logs. Species have been found to be blind and living in caves, or cavernicolous, reported to be found on the island of Hawaii and in South Africa. Food typically consists of a wide array of living and dead plant and animal matter.^[20] For protection from predators, the species *Doru taeniatum* of earwigs can squirt foul-smelling yellow liquid in the form of jets from scent glands on the dorsal side of the third and fourth abdominal segment. It aims the discharges by revolving the abdomen, a maneuver that enables it simultaneously to use its pincers in defense.^[24]

Ecology

Earwigs are mostly scavengers, but some are omnivorous or predatory.^{[7]:739–740} The abdomen of the earwig is flexible and muscular. It is capable of maneuvering as well as opening and closing the forceps. The forceps are used for a variety of purposes. In some species, the forceps have been observed in use for holding prey, and in copulation. The forceps tend to be more curved in males than in females.^[25]



A male of *Forficula auricularia* feeding on flowers.

The common earwig is an omnivore, eating plants and ripe fruit as well as actively hunting arthropods. To a large extent, this species is also a scavenger, feeding on decaying plant and animal matter if given the chance. Observed prey include largely plant lice, but also large insects such as bluebottle flies and woolly aphids.^[10] Plants that they feed on typically include clover, dahlias, zinnias, butterfly bush, hollyhock, lettuce, cauliflower, strawberry, blackberry, sunflowers, celery, peaches, plums, grapes, potatoes, roses, seedling beans and beets, and tender grass shoots and roots; they have also been known to eat corn silk, damaging the corn.^[26]

Species of the suborders Arixeniina and Hemimerina are generally considered epizoic, or living on the outside of other animals, mainly mammals. In the Arixeniina, family Arixeniidae, species of the genus *Arixenia* are normally found deep in the skin folds and gular pouch of Malaysian hairless bulldog bats (*Cheiromeles torquatus*), apparently feeding on bats' body or glandular secretions. On the other hand, species in the genus *Xeniaria* (still of the suborder Arixeniina) are believed to feed on the guano and possibly the guanophilous arthropods in the bat's roost, where it has been found. Hemimerina includes *Araeomerus* found in the nest of Long-tailed pouch rats (*Beamys*), and *Hemimerus* which are found on Giant *Cricetomys* rats.^{[16][27]}

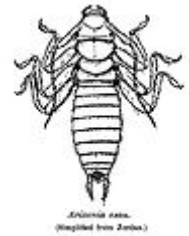
Earwigs are generally nocturnal, and typically hide in small, dark, and often moist areas in the daytime. They can usually be seen on household walls and ceilings. Interaction with earwigs at this time results in a defensive free-fall to the ground followed by a scramble to a nearby cleft or crevice.^[25] During the summer they can be found around damp areas such as near sinks and in bathrooms. Earwigs tend to gather in shady cracks or openings or anywhere that they can remain concealed during daylight. Picnic tables, compost and waste bins, patios, lawn furniture, window frames, or anything with minute spaces (even artichoke blossoms) can potentially harbour them.^[28]

Predators and parasites

Earwigs are regularly preyed upon by birds, and like many other insect species they are prey for insectivorous mammals, amphibians, lizards, centipedes, assassin bugs, and spiders.^[29] European naturalists have observed bats preying upon earwigs.^[29] Their primary insect predators are parasitic species of Tachinidae, or tachinid flies, whose larvae are endoparasites. One species of tachinid fly, *Triarthria setipennis*, has been demonstrated to be successful as a biological control of earwigs for almost a century.^{[30][31]} Another tachinid fly and parasite of earwigs, *Ocytata pallipes*, has shown promise as a biological control agent as well.^[32] The common predatory wasp, the yellow jacket (*Vespula maculifrons*), preys upon earwigs when abundant.^[33] A small species of roundworm, *Mermis nigrescens*, is known to occasionally parasitize earwigs that have consumed roundworm eggs with plant matter.^[34] At least 26 species of parasitic fungus from the order Laboulbeniales have been found on earwigs.^[35] The eggs and nymphs are also cannibalized by other earwigs.^[36] A species of tyroglyphoid mite, *Histiostoma polypori* (Histiostomatidae, Astigmata), are observed on common earwigs, sometimes in great densities;^[37] however, this mite feeds on earwig cadavers and not its live earwig transportation.^[38] Hippolyte Lucas observed scarlet acarine mites on European earwigs.^[39]

Evolution

The fossil record of the Dermaptera starts in the Late Triassic to Early Jurassic period about 208 million years ago in England and Australia, and comprises about 70 specimens in the extinct suborder Archidermaptera. Some of the traits believed by neontologists to belong to modern earwigs are not found in the earliest fossils, but adults had five-segmented tarsi (the final segment of the leg), well developed ovipositors, veined tegmina (forewings) and long segmented cerci; in fact the pincers would not have been curled or used as they are now.^[14] The theorized stem group of the Dermaptera are the Protelytroptera. These insects, which resemble modern Blattodea, or cockroaches owing to shell-like forewings and the large, unequal anal fan, are known from the Permian of North America, Europe and Australia. There are no fossils from the Triassic when the morphological changes from Protelytroptera to Dermaptera took place.^[42] The most likely, and most closely resembling, related order of insects is Notoptera, theorized by Giles in 1963. However, other arguments have been made by other authors



Arixenia esau
from the extinct
suborder
Arixeniina



Hemimerus hansenii
from the extinct
suborder
Hemimerina

linking them to Phasmida, Embioptera, Plecoptera, and Dictyoptera.^[11]

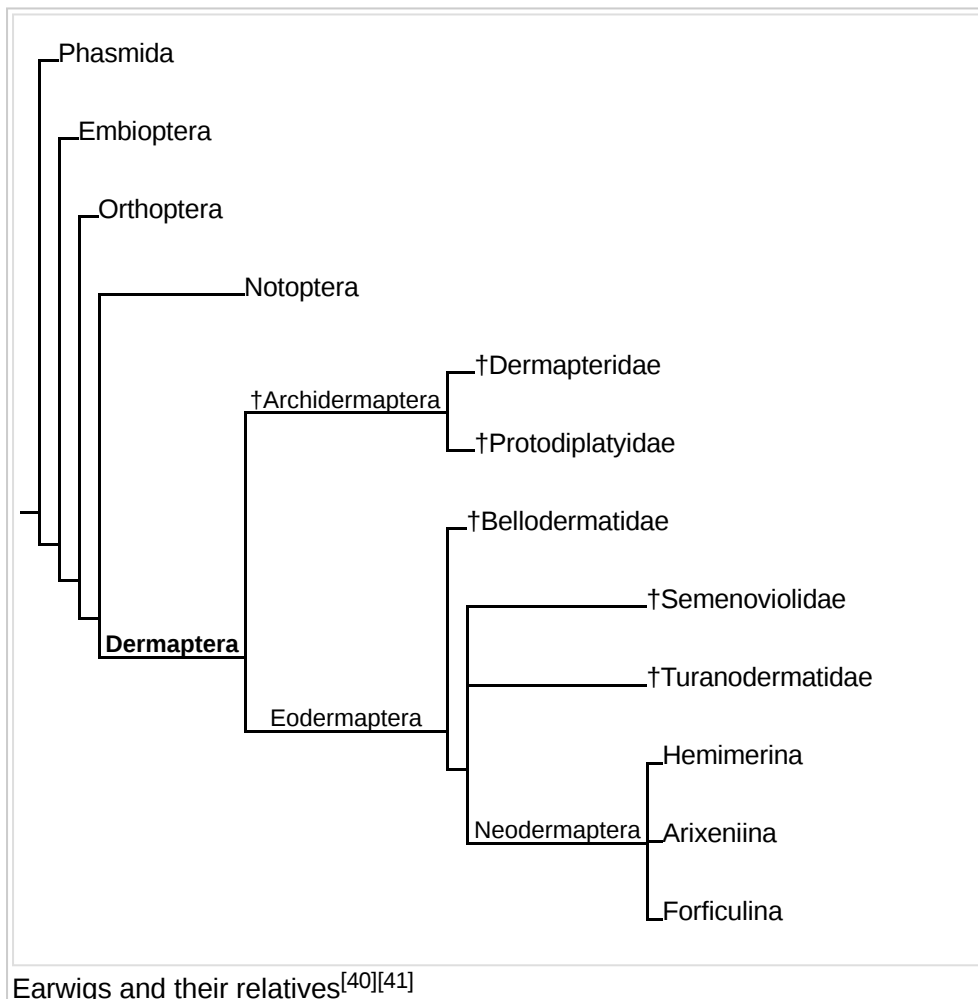
Archidermaptera is believed to be sister to the remaining earwig groups, the extinct Eodermaptera and the living suborder Neodermaptera (= former suborders Forficulina, Hemimerina, and Arixeniina).

The extinct suborders have

tarsi with five segments (unlike the three found in Neodermaptera) as well as unsegmented cerci. No fossil Hemimeridae and Arixeniidae are known.^[43] Species in Hemimeridae were at one time in their own order, Diploglassata, Dermodermaptera, or Hemimerina. Like most other epizoid species, there is no fossil record, but they are probably no older than late Tertiary.^[14]

Some evidence of early evolutionary history is the structure of the antennal heart, a separate circulatory organ consisting of two ampullae, or vesicles,^[44] that are attached to the frontal cuticle to the bases of the antennae.^[45] These features have not been found in other insects. An independent organ exists for each antenna, consisting of an ampulla, attached to the frontal cuticle medial to the antenna base and forming a thin-walled sac with a valved ostium on its ventral side. They pump blood by elastic connective tissue, rather than muscle.^[46]

Molecular studies suggest that this order is the sister to Plecoptera or to Ephemeroptera.^[47]



Earwigs and their relatives^{[40][41]}

Taxonomy

Distinguishing characteristics

The characteristics which distinguish the order Dermaptera from other insect orders are:^[48]

- *General body shape*: Elongate; dorso-ventrally flattened.
- *Head*: Prognathous. Antennae are segmented. Biting-type mouthparts. Ocelli absent. Compound eyes in most species, reduced or absent in some taxa.
- *Appendages*: Two pairs of wings normally present. The forewings are modified into short smooth, veinless tegmina. Hindwings are membranous and semicircular with veins radiating outwards.
- *Abdomen*: Cerci are unsegmented and resemble forceps. The ovipositor in females is reduced or absent.

The overwhelming majority of earwig species are in Forficulina, grouped into nine families of 180 genera,^[42] including *Forficula auricularia*, the common European Earwig. Species within Forficulina are free-living, have functional wings and are not parasites. The cerci are unsegmented and modified into large, forceps-like structures.

The first epizootic species of earwig was discovered by a London taxidermist on the body of a Malaysian hairless bulldog bat in 1909, then described by Karl Jordan. By the 1950s, the two suborders *Arixeniina* and *Hemimerina* had been added to Dermaptera.^[16]

Arixeniina represents two genera, *Arixenia* and *Xeniaria*, with a total of five species in them. As with Hemimerina, they are blind and wingless, with filiform segmented cerci. Hemimerina are viviparous ectoparasites, preferring the fur of African rodents in either *Cricetomys* or *Beamys* genera.^[43] Hemimerina also has two genera, *Hemimerus* and *Araeomerus*, with a total of 11 species.^[43]

Phylogeny

Dermaptera is relatively small compared to the other orders of Insecta, with only about 2,000 species, 3 suborders and 15 families, including the extinct suborders Archidermaptera and Eodermaptera with their extinct families Protodiplatyidae, Dermapteridae, Semenoviidae, and Turanodermatidae. The phylogeny of the Dermaptera is still debated. The extant Dermaptera appear to be monophyletic and there is support for the monophyly of the families Forficulidae, Chelisochidae, Labiduridae and Anisolabididae, however evidence has supported the conclusion that the former suborder Forficulina was paraphyletic through the exclusion of Hemimerina and Arixeniina which should instead be nested within the Forficulina.^{[42][49]} Thus, these former suborders were eliminated in the most recent higher classification.

Relationship with humans

Earwigs are fairly abundant and are found in many areas around the world. There is no evidence that they transmit diseases to humans or other animals. Their pincers are commonly believed to be dangerous, but in reality, even the curved pincers of males cause little or no harm to humans.^[50] Earwigs have been rarely known^[51] to crawl into the ears of humans, but they do not lay eggs inside the human body or human brain.^{[52][53]}



A female of the common earwig in a threat pose

There is a debate whether earwigs are harmful or beneficial to crops, as they eat both the foliage and the insects eating such foliage, such as aphids, though it would take a large population to do considerable damage. The common earwig eats a wide variety of plants, and also a wide variety of foliage, including the leaves and petals. They have been known to cause economic losses in fruit and vegetable crops. Some examples are the flowers, hops, red raspberries,^[54] and corn crops in Germany, and in the south of France, earwigs have been observed feeding on peaches and apricots. The earwigs attacked mature plants and made cup-shaped bite marks 3–11 mm (0.12–0.43 in) in diameter.^[55]

In literature and folklore

- Oscar Cook wrote the short story (appearing in *Switch On The Light*, April, 1931; *A Century Of Creepy Stories* 1934; *Pan Horror* 2, 1960) *Boomerang*, which was later adapted by Rod Serling for the Night Gallery tv-series episode, *The Caterpillar*.^[56] It tells the tale of the use of an earwig as a murder instrument applied by a man obsessed with the wife of an associate.
- Robert Herrick in *Hesperides* describes a feast attended by Queen Titania through writing: "Beards of mice, a newt's stew'd thigh, A bloated Earwig and a fly".
- Thomas Hood discusses the myth of earwigs finding shelter in the human ear in the poem "Love Lane" by saying the following: "'Tis vain to talk of hopes and fears, / And hope the least reply to wing, / From any maid that stops her ears / In dread of earwigs creeping in!"^[57]
- In some parts of rural England the earwig is called "battle-twig", which is present in Alfred, Lord Tennyson's poem *The Spinster's Sweet-Arts*: "'Twur as bad as battle-twig 'ere i' my oan blue chamber to me."^[58]
- In some regions of Japan, earwigs are called "Chinpo-Basami" or "Chinpo-Kiri", which means "penis cutter". Kenta Takada, a Japanese cultural entomologist, has inferred that these names may be derived from the fact that earwigs were seen around old Japanese-style toilets.^[59]
- In George's Marvellous Medicine, George's Grandma encourages him to eat unwashed celery with beetles and earwigs still on them. "A big fat earwig is very tasty," Grandma said, licking her lips. 'But you've got to be very quick, my dear, when you put one of those in your mouth. It has a pair of sharp nippers on its back end and if it grabs your tongue with those, it never lets go. So you've got to bite the earwig first, chop chop, before it bites you."^[60]

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Fly

True **flies** are insects of the order **Diptera**, the name being derived from the Greek δι- *di-* "two", and πτερόν *pteron* "wings". Insects of this order use only a single pair of wings to fly, the hindwings having evolved into advanced mechanosensory organs known as halteres, which act as high-speed sensors of rotational movement and allow dipterans to perform advanced aerobatics.^[1] Diptera is a large order containing an estimated 1,000,000 species including horse-flies,^[a] crane flies, hoverflies and others, although only about 125,000 species have been described.^[4]

Flies have a mobile head, with a pair of large compound eyes, and mouthparts designed for piercing and sucking (mosquitoes, black flies and robber flies), or for lapping and sucking in the other groups. Their wing arrangement gives them great maneuverability in flight, and claws and pads on their feet enable them to cling to smooth surfaces. Flies undergo complete metamorphosis; the eggs are laid on the larval food-source and the larvae, which lack true limbs, develop in a protected environment, often inside their food source. The pupa is a tough capsule from which the adult emerges when ready to do so; flies mostly have short lives as adults.

Diptera is one of the major insect orders and of considerable ecological and human importance. Flies are important pollinators, second only to the bees and their Hymenopteran relatives. Flies may have been among the evolutionarily earliest pollinators responsible for early plant pollination. Fruit flies are used as model organisms in research, but less benignly, mosquitoes are vectors for malaria, dengue, West Nile fever, yellow fever, encephalitis, and other infectious diseases; and houseflies, commensal with humans all over the world, spread food-borne illnesses. Flies can be annoyances especially in some parts of the world where they can occur in large numbers, buzzing and settling on the skin or eyes to bite or seek fluids. Larger flies such as tsetse flies and screwworms cause significant economic harm to cattle. Blowfly larvae, known as gentles, and other dipteran larvae, known more generally as maggots, are used as fishing bait and as food for carnivorous animals. They are also used in medicine in debridement to clean wounds.

Contents

Taxonomy and phylogeny

- Relationships to other insects
- Relationships between fly subgroups and families
- Diversity

Anatomy and morphology

- Flight

Fly

Temporal range: 245 –0 Ma

PreЄ

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S

D

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PgN

Middle Triassic – Recent



Syrphus ribesii, showing characteristic dipteran features: large eyes, small antennae, sucking mouthparts, single pair of flying wings, hindwings reduced to clublike halteres

Scientific classification

Kingdom:

Animalia

Phylum:

Arthropoda

Class:

Insecta

Superorder:

Panorpida

(unranked):

Antliophora

Order:

Diptera

Linnaeus, 1758

Life cycle and development

Larva

Pupa

Adult

Ecology

Anti-predator adaptations

In culture

Symbolism

Economic importance

Uses

Notes

References

Further reading

External links

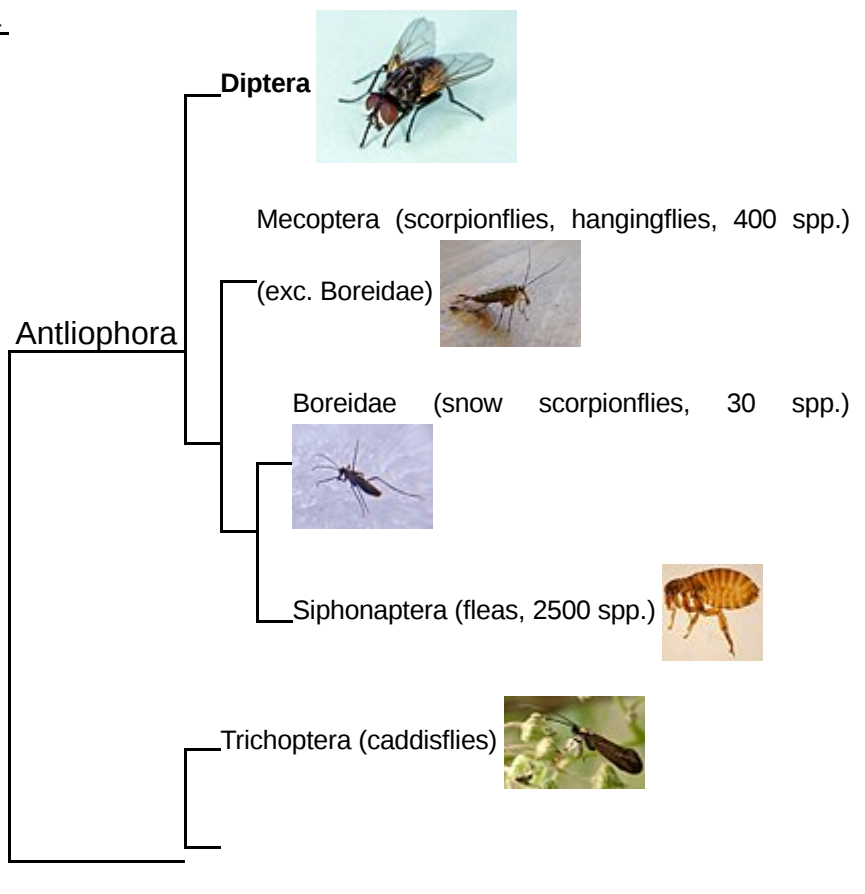
Taxonomy and phylogeny

Relationships to other insects

Dipterans are endopterygotes, insects that undergo radical metamorphosis. They belong to the Mecopterida, alongside the Mecoptera, Siphonaptera, Lepidoptera and Trichoptera.^{[5][6]} The possession of a single pair of wings distinguishes most true flies from other insects with "fly" in their names. However, some true flies such as Hippoboscidae (louse flies) have become secondarily wingless.^[7]

The cladogram represents the current consensus view.^[8]

part of Endopterygota Mecopterida



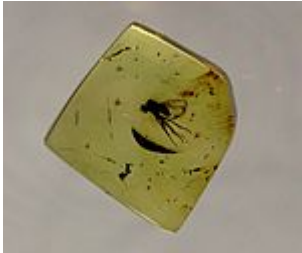
Lepidoptera (butterflies and moths)



Hymenoptera (sawflies, wasps, ants, bees)



Relationships between fly subgroups and families



Fossil brachyceran in Baltic amber. Lower Eocene, c. 50 million years ago

The first true dipterans known are from the Middle Triassic (around 240 million years ago), and they became widespread during the Middle and Late Triassic.^[9] Modern flowering plants did not appear until the Cretaceous (around 140 million years ago), so the original dipterans must have had a different source of nutrition other than nectar. Based on the attraction of many modern fly groups to shiny droplets, it has been suggested that they may have fed on honeydew produced by sap-sucking bugs which were abundant at the time, and dipteran mouthparts are well-adapted to softening and lapping up the crusted residues.^[10] The basal clades in the Diptera include the Deuterophlebiidae and the enigmatic



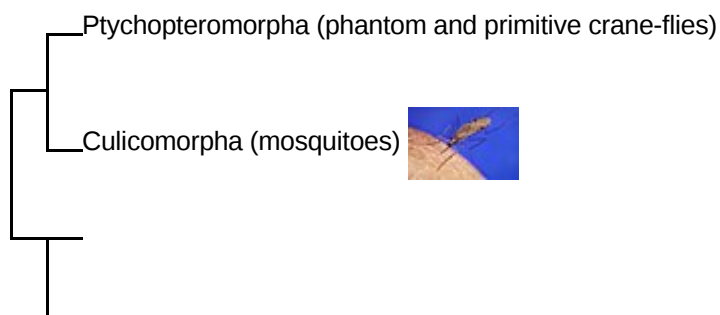
Fossil nematoceran in Dominican amber. Sandfly, *Lutzomyia adiketis* (Psychodidae), Early Miocene, c. 20 million years ago

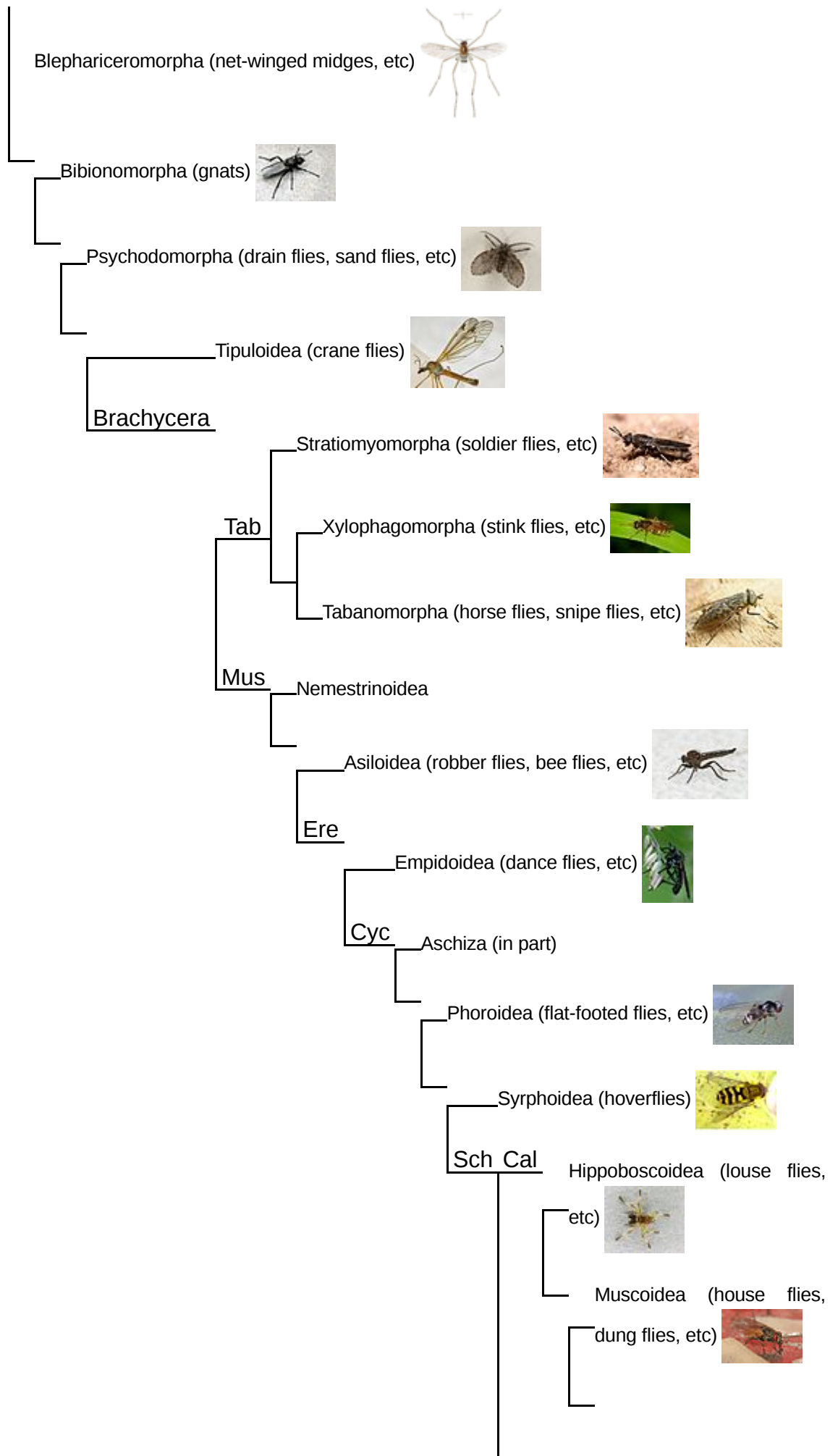
Nymphomyiidae.^[11] Three episodes of evolutionary radiation are thought to have occurred based on the fossil record. Many new species of lower Diptera developed in the Triassic, about 220 million years ago. Many lower Brachycera appeared in the Jurassic, some 180 million years ago. A third radiation took place among the Schizophora at the start of the Paleogene, 66 million years ago.^[11]

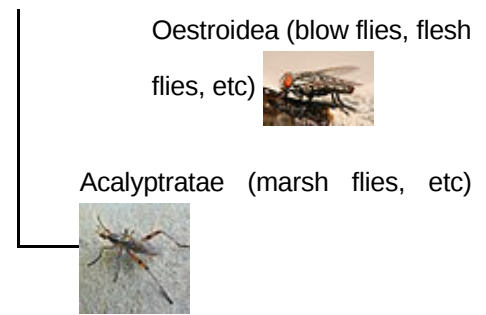
The phylogenetic position of Diptera has been controversial. The monophyly of holometabolous insects has long been accepted, with the main orders being established as Lepidoptera, Coleoptera, Hymenoptera and Diptera, and it is the relationships between these groups which has caused difficulties. Diptera is widely thought to be a member of Mecopterida, along with Lepidoptera (butterflies and moths), Trichoptera (caddisflies), Siphonaptera (fleas), Mecoptera (scorpionflies) and possibly Strepsiptera (twisted-wing flies). Diptera has been grouped with Siphonaptera and Mecoptera in the Antliophora, but this has not been confirmed by molecular studies.^[12]

Diptera were traditionally broken down into two suborders, Nematocera and Brachycera, distinguished by the differences in antennae. The Nematocera are identified by their elongated bodies and many-segmented, often feathery antennae as represented by mosquitoes and crane flies. The Brachycera have rounder bodies and much shorter antennae.^{[13][14]} Subsequent studies have identified the Nematocera as being non-monophyletic with modern phylogenies placing the Brachycera within grades of groups formerly placed in the Nematocera. The construction of a phylogenetic tree has been the subject of ongoing research. The following cladogram is based on the FLYTREE project.^{[11][15][16]}

Nematocera







Abbreviations used in the cladogram:

- Cal=Calypttratae
- Cyc=Cyclorrhapha
- Ere=Eremoneura
- Mus=Muscomorpha
- Sch=Schizophora
- Tab=Tabanomorpha

Diversity

Flies are often abundant and are found in almost all terrestrial habitats in the world apart from Antarctica. They include many familiar insects such as house flies, blow flies, mosquitoes, gnats, black flies, midges and fruit flies. More than 150,000 have been formally described and the actual species diversity is much greater, with the flies from many parts of the world yet to be studied intensively.^{[17][18]} The suborder Nematocera include generally small, slender insects with long antennae such as mosquitoes, gnats, midges and crane-flies, while the Brachycera includes broader, more robust flies with short antennae. Many nematoceran larvae are aquatic.^[19] There are estimated to be a total of about 19,000 species of Diptera in Europe, 22,000 in the Nearctic region, 20,000 in the Afrotropical region, 23,000 in the Oriental region and 19,000 in the Australasian region.^[20] While most species have restricted distributions, a few like the housefly (*Musca domestica*) are cosmopolitan.^[21] *Gauromydas heros* (Asiloidea), with a length of up to 7 cm (2.8 in), is generally considered to be the largest fly in the world,^[22] while the smallest is *Euryplatea nanaknihali*, which at 0.4 mm (0.016 in) is smaller than a grain of salt.^[23]



Gauromydas heros is the largest fly in the world.

Brachycera are ecologically very diverse, with many being predatory at the larval stage and some being parasitic. Animals parasitised include molluscs, woodlice, millipedes, insects, mammals,^[20] and amphibians.^[24] Flies are the second largest group of pollinators after the Hymenoptera (bees, wasps and relatives). In wet and colder environments flies are significantly more important as pollinators. Compared to bees, they need less food as they do not need to provision their young. Many flowers that bear low nectar and those that have evolved trap pollination depend on flies.^[25] It is thought that some of the earliest pollinators of plants may have been flies.^[26]

The greatest diversity of gall forming insects are found among the flies, principally in the family Cecidomyiidae (gall midges).^[27] Many flies (most importantly in the family Agromyzidae) lay their eggs in the mesophyll tissue of leaves with larvae feeding between the surfaces forming blisters and mines.^[28] Some families are mycophagous or fungus feeding. These include the cave dwelling Mycetophilidae (fungus gnats) whose larvae are the only diptera with bioluminescence. The Sciaridae are also fungus feeders. Some plants are pollinated by fungus feeding flies that visit fungus infected male flowers.^[29]

The larvae of *Megaselia scalaris* (Phoridae) are almost omnivorous and consume such substances as paint and shoe polish.^[30] The *Exorista mella* (Walker) fly are considered generalists and parasitoids of a variety of hosts^[31]. The larvae of the shore flies (Ephydriidae) and some Chironomidae survive in extreme environments including glaciers (*Diamesa* sp., Chironomidae^[32]), hot springs, geysers, saline pools, sulphur pools, septic tanks and even crude oil (*Helaeomyia petrolei*^[32]).^[20] Adult hoverflies (Syrphidae) are well known for their mimicry and the larvae adopt diverse lifestyles including being inquiline scavengers inside the nests of social insects.^[33] Some brachycerans are agricultural pests, some bite animals and humans and suck their blood, and some transmit diseases.^[20]

Anatomy and morphology

Flies are adapted for aerial movement and typically have short and streamlined bodies. The first tagma of the fly, the head, bears the eyes, the antennae, and the mouthparts (the labrum, labium, mandible, and maxilla make up the mouthparts). The second tagma, the thorax, bears the wings and contains the flight muscles on the second segment, which is greatly enlarged; the first and third segments have been reduced to collar-like structures, and the third segment bears the halteres, which help to balance the insect during flight. The third tagma is the abdomen consisting of 11 segments, some of which may be fused, and with the 3 hindmost segments modified for reproduction.^[34] Some Dipterans are mimics and can only be distinguished from their models by very careful inspection. An example of this is *Spilomyia longicornis*, which is a fly but mimics a vespid wasp.



Head of a horse-fly showing large compound eyes and stout piercing mouthparts

Flies have a mobile head with a pair of large compound eyes on the sides of the head, and in most species, three small ocelli on the top. The compound eyes may be close together or widely separated, and in some instances are divided into a dorsal region and a ventral region, perhaps to assist in swarming behaviour. The antennae are well-developed but variable, being thread-like, feathery or comb-like in the different families. The mouthparts are adapted for piercing and sucking, as in the black flies, mosquitoes and robber flies, and for lapping and sucking as in many other groups.^[34] Female horse-flies use knife-like mandibles and maxillae to make a cross-shaped incision in the host's skin and then lap up the blood that flows. The gut includes large diverticulae, allowing the insect to store small quantities of liquid after a meal.^[35]

For visual course control, flies' optic flow field is analyzed by a set of motion-sensitive neurons.^[36] A subset of these neurons is thought to be involved in using the optic flow to estimate the parameters of self-motion, such as yaw, roll, and sideward translation.^[37] Other neurons are thought to be involved in analyzing the content of the visual scene itself, such as separating figures from the ground using motion parallax.^{[38][39]} The H1 neuron is responsible for detecting horizontal motion across the entire visual field of the fly, allowing the fly to generate and guide stabilizing motor corrections midflight with respect to yaw.^[40] The ocelli are concerned in the detection of changes in light intensity, enabling the fly to react swiftly to the approach of an object.^[41]

Like other insects, flies have chemoreceptors that detect smell and taste, and mechanoreceptors that respond to touch. The third segments of the antennae and the maxillary palps bear the main olfactory receptors, while the gustatory receptors are in the labium, pharynx, feet, wing margins and female genitalia,^[42] enabling flies to taste their food by walking on it. The taste receptors in females at the tip of the abdomen receive information on the suitability of a site for ovipositing.^[41] Flies that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts, and many blood-sucking flies can detect the raised concentration of carbon dioxide that occurs near large animals.^[43] Some tachinid flies (Ormiinae) which are parasitoids of bush crickets, have sound receptors to help them locate their singing hosts.^[44]

Diptera have one pair of fore wings on the mesothorax and a pair of halteres, or reduced hind wings, on the metathorax. A further adaptation for flight is the reduction in number of the neural ganglia, and concentration of nerve tissue in the thorax, a feature that is most extreme in the highly derived Muscomorpha infraorder.^[35] Some species of flies are exceptional in that they are

secondarily flightless. The only other order of insects bearing a single pair of true, functional wings, in addition to any form of halteres, are the Strepsiptera. In contrast to the flies, the Strepsiptera bear their halteres on the mesothorax and their flight wings on the metathorax.^[45] Each of the fly's six legs has a typical insect structure of coxa, trochanter, femur, tibia and tarsus, with the tarsus in most instances being subdivided into five tarsomeres.^[34] At the tip of the limb is a pair of claws, and between these are cushion-like structures known as pulvilli which provide adhesion.^[46]

The abdomen shows considerable variability among members of the order. It consists of eleven segments in primitive groups and ten segments in more derived groups, the tenth and eleventh segments having fused.^[47] The last two or three segments are adapted for reproduction. Each segment is made up of a dorsal and a ventral sclerite, connected by an elastic membrane. In some females, the sclerites are rolled into a flexible, telescopic ovipositor.^[34]



A crane fly, showing the hind wings reduced to drumstick-shaped halteres

Flight

Flies are capable of great manoeuvrability during flight due to the presence of the halteres. These act as gyroscopic organs and are rapidly oscillated in time with the wings; they act as a balance and guidance system by providing rapid feedback to the wing-steering muscles, and flies deprived of their halteres are unable to fly. The wings and halteres move in synchrony but the amplitude of each wing beat is independent, allowing the fly to turn sideways.^[48] The wings of the fly are attached to two kinds of muscles, those used to power it and another set used for fine control.^[49]



Tabanid fly in flight

Flies tend to fly in a straight line then make a rapid change in direction before continuing on a different straight path. The directional changes are called saccades and typically involve an angle of 90°, being achieved in 50 milliseconds. They are initiated by visual stimuli as the fly observes an object, nerves then activate steering muscles in the thorax that cause a small change in wing stroke which generate sufficient torque to turn. Detecting this within four or five wingbeats, the halteres trigger a counter-turn and the fly heads off in a new direction.^[50]

Flies have rapid reflexes that aid their escape from predators but their sustained flight speeds are low. Dolichopodid flies in the genus *Condylostylus* respond in less than 5 milliseconds to camera flashes by taking flight.^[51] In the past, the deer bot fly, *Cephenemyia*, was claimed to be one of the fastest insects on the basis of an estimate made visually by Charles Townsend in 1927.^[52] This claim, of speeds of 600 to 800 miles per hour, was regularly repeated until it was shown to be physically impossible as well as incorrect by Irving Langmuir. Langmuir suggested an estimated speed of 25 miles per hour.^{[53][54][55]}

Although most flies live and fly close to the ground, a few are known to fly at heights and a few like *Oscinella* (Chloropidae) are known to be dispersed by winds at altitudes of up to 2000 ft and over long distances.^[56] Some hover flies like *Metasyrphus corollae* have been known to undertake long flights in response to aphid population spurts.^[57]

Males of fly species such as *Cuterebra*, many hover flies,^[58] bee flies (Bombyliidae)^[59] and fruit flies (Tephritidae)^[60] maintain territories within which they engage in aerial pursuit to drive away intruding males and other species.^[61] While these territories may be held by individual males, some species, such as *A. freeborni*,^[62] form leks with many males aggregating in displays.^[60] Some flies maintain an airspace and still others form dense swarms that maintain a stationary location with respect to landmarks. Many flies mate in flight while swarming.^[63]

Life cycle and development

Diptera go through a complete metamorphosis with four distinct life stages – egg, larva, pupa and adult.

Larva

In many flies, the larval stage is long and adults may have a short life. Most dipteran larvae develop in protected environments; many are aquatic and others are found in moist places such as carrion, fruit, vegetable matter, fungi and, in the case of parasitic species, inside their hosts. They tend to have thin cuticles and become desiccated if exposed to the air. Apart from the Brachycera, most dipteran larvae have sclerotinised head capsules, which may be reduced to remnant mouth hooks; the Brachycera, however, have soft, gelatinized head capsules from which the sclerites are reduced or missing. Many of these larvae retract their heads into their thorax.^{[34][64]}



Mating anthomyiid flies



Life cycle of stable fly *Stomoxys calcitrans*, showing eggs, 3 larval instars, pupa, and adult

Some other anatomical distinction exists between the larvae of the Nematocera and the Brachycera. Especially in the Brachycera, little demarcation is seen between the thorax and abdomen, though the demarcation may be visible in many Nematocera, such as mosquitoes; in the Brachycera, the head of the larva is not clearly distinguishable from the rest of the body, and few, if any, sclerites are present. Informally, such brachyceran larvae are called maggots,^[65] but the term is not technical and often applied indifferently to fly larvae or insect larvae in general. The eyes and antennae of brachyceran larvae are reduced or absent, and the abdomen also lacks appendages such as cerci. This lack of features is an adaptation to food such as carrion, decaying detritus, or host tissues surrounding endoparasites.^[35] Nematoceran larvae generally have well-developed eyes and antennae, while those of Brachyceran larvae are reduced or modified.^[66]

Dipteran larvae have no jointed, "true legs",^[64] but some dipteran larvae, such as species of Simuliidae, Tabanidae and Vermileonidae, have prolegs adapted to hold onto a substrate in flowing water, host tissues or prey.^[67] The majority of

dipterans are oviparous and lay batches of eggs, but some species are ovoviviparous, where the larvae starting development inside the eggs before they hatch or viviparous, the larvae hatching and maturing in the body of the mother before being externally deposited. These are found especially in groups that have larvae dependent on food sources that are short-lived or are accessible for brief periods.^[68] This is widespread in some families such as the Sarcophagidae. In *Hylemya strigosa* (Anthomyiidae) the larva moults to the second instar before hatching, and in *Termitoxenia* (Phoridae) females have incubation pouches, and a full developed third instar larva is deposited by the adult and it almost immediately pupates with no freely feeding larval stage. The tsetse fly (as well as other Glossinidae, Hippoboscidae, Nycteribidae and Streblidae) exhibits adenotrophic viviparity; a single fertilised egg is retained in the oviduct and the developing larva feeds on glandular secretions. When fully grown, the female finds a spot with soft soil and the larva works its way out of the oviduct, buries itself and pupates. Some flies like *Lundstroemia parthenogenetica* (Chironomidae) reproduce by thelytokous parthenogenesis, and some gall midges have larvae that can produce eggs (paedogenesis).^{[69][70]}

Pupa

The pupae take various forms. In some groups, particularly the Nematocera, the pupa is intermediate between the larval and adult form; these pupae are described as "obtect", having the future appendages visible as structures that adhere to the pupal body. The outer surface of the pupa may be leathery and bear spines, respiratory features or locomotory paddles. In other groups, described as "coarctate", the appendages are not visible. In these, the outer surface is a puparium, formed from the last larval skin, and the actual pupa is concealed within. When the adult insect is ready to emerge from this tough, desiccation-resistant capsule, it inflates a balloon-like structure on its head, and forces its way out.^[34]

Adult

The adult stage is usually short, its function only to mate and lay eggs. The genitalia of male flies are rotated to a varying degree from the position found in other insects.^[71] In some flies, this is a temporary rotation during mating, but in others, it is a permanent torsion of the organs that occurs during the pupal stage. This torsion may lead to the anus being below the genitals, or, in the case of 360° torsion, to the sperm duct being wrapped around the gut and the external organs being in their usual position. When flies mate, the male initially flies on top of the female, facing in the same direction, but then turns around to face in the opposite direction. This forces the male to lie on his back for his genitalia to remain engaged with those of the female, or the torsion of the male genitals allows the male to mate while remaining upright. This leads to flies having more reproduction abilities than most insects, and much quicker. Flies occur in large populations due to their ability to mate effectively and quickly during the mating season.^[35]

Ecology

As ubiquitous insects, dipterans play an important role at various trophic levels both as consumers and as prey. In some groups the larvae complete their development without feeding, and in others the adults do not feed. The larvae can be herbivores, scavengers, decomposers, predators or parasites, with the consumption of decaying organic matter being one of the most prevalent feeding behaviours. The fruit or detritus is consumed along with the associated micro-organisms, a sieve-like filter in the pharynx being used to concentrate the particles, while flesh-eating larvae have mouth-hooks to help shred their food. The larvae of some groups feed on or in the living tissues of plants and fungi, and some of these are serious pests of agricultural crops. Some aquatic larvae consume the films of algae that form underwater on rocks and plants. Many of the parasitoid larvae grow inside and eventually kill other arthropods, while parasitic larvae may attack vertebrate hosts.^[34]

Whereas many dipteran larvae are aquatic or live in enclosed terrestrial locations, the majority of adults live above ground and are capable of flight. Predominantly they feed on nectar or plant or animal exudates, such as honeydew, for which their lapping mouthparts are adapted. The flies that feed on vertebrate blood have sharp stylets that pierce the skin, the insects inserting anticoagulant saliva and absorbing the blood that flows; in this process, certain diseases can be transmitted. The bot flies (Oestridae) have evolved to parasitize mammals. Many species complete their life cycle inside the bodies of their hosts.^[72] In many dipteran groups, swarming is a feature of adult life, with clouds of insects gathering in certain locations; these insects are mostly males, and the swarm may serve the purpose of making their location more visible to females.^[34]

Anti-predator adaptations

Flies are eaten by other animals at all stages of their development. The eggs and larvae are parasitised by other insects and are eaten by many creatures, some of which specialise in feeding on flies but most of which consume them as part of a mixed diet. Birds, bats, frogs, lizards, dragonflies and spiders are among the predators of flies.^[73] Many flies have evolved mimetic resemblances that aid their protection. Batesian mimicry is widespread with many hoverflies resembling bees and wasps,^{[74][75]} ants^[76] and some species of tephritid fruit fly resembling spiders.^[77] Some species of hoverfly are myrmecophilous, their young live and grow within the nests of ants. They are protected from the ants by imitating chemical odours given by ant colony members.^[78] Bombyliid bee flies such as *Bombylius major* are short-bodied, round, furry, and distinctly bee-like as they visit flowers for nectar, and are likely also Batesian mimics of bees.^[79]

In contrast, *Drosophila subobscura*, a species of fly in the genus *Drosophila*, lacks a category of hemocytes that are present in other studied species of *Drosophila*, leading to an inability to defend against parasitic attacks, a form of innate immunodeficiency.^[80]

In culture

Symbolism



Petrus Christus's 1446 painting *Portrait of a Carthusian* has a fly painted on a trompe l'oeil frame.

Flies play a variety of symbolic roles in different cultures. These include both positive and negative roles in religion. In the traditional Navajo religion, Big Fly is an important spirit being.^{[81][82][83]} In Christian demonology, Beelzebub is a demonic fly, the "Lord of the Flies", and a god of the Philistines.^{[84][85][86]}

Flies have appeared in literature since ancient Sumer.^[87] In a Sumerian poem, a fly helps the goddess Inanna when her husband Dumuzid is being chased by *galla* demons.^[87] In the Mesopotamian versions of the flood myth, the dead corpses floating on the waters are compared to flies.^[87] Later, the gods are said to swarm "like flies" around the hero Utnapishtim's offering.^[87] Flies appear on Old Babylonian seals as symbols of Nergal, the god of death.^[87] Fly-shaped lapis lazuli beads were often worn in ancient Mesopotamia, along with other kinds of fly-jewellery.^[87]

In *Prometheus Bound*, which is attributed to the Athenian tragic playwright Aeschylus, a gadfly sent by Zeus's wife Hera pursues and torments his mistress Io, who has been transformed into a cow and is watched constantly by the hundred eyes of the herdsman

Argus.^{[88][89]} "Io: Ah! Hah! Again the prick, the stab of gadfly-sting! O earth, earth, hide the hollow shape—Argus—that evil thing—the hundred-eyed."^[89] William Shakespeare, inspired by Aeschylus, has Tom o'Bedlam in *King Lear*, "Whom the foul fiend hath led through fire and through flame, through ford and whirlpool, o'er bog and quagmire", driven mad by the constant pursuit.^[89] In *Antony and Cleopatra*, Shakespeare similarly likens Cleopatra's hasty departure from the Actium battlefield to that of a cow chased by a gadfly.^[90] More recently, in 1962 the biologist Vincent Dethier wrote *To Know a Fly*, introducing the general reader to the behaviour and physiology of the fly.^[91]

Flies appear in popular culture in concepts such as fly-on-the-wall documentary-making in film and television production. The metaphoric name suggests that events are seen candidly, as a fly might see them.^[92] Flies have inspired the design of miniature flying robots.^[93] Steven Spielberg's 1993 film *Jurassic Park* relied on the idea that DNA could be preserved in the stomach contents of a blood-sucking fly fossilised in amber, though the mechanism has been discounted by scientists.^[94]

Economic importance

Dipterans are an important group of insects and have a considerable impact on the environment. Some leaf-miner flies (Agromyzidae), fruit flies (Tephritidae and Drosophilidae) and gall midges (Cecidomyiidae) are pests of agricultural crops; others such as tsetse flies, screwworm and botflies (Oestridae) attack livestock, causing wounds, spreading disease, and creating significant economic harm. See article: Parasitic flies of domestic animals. A few can even cause myiasis in humans. Still others such as mosquitoes (Culicidae), blackflies (Simuliidae) and drain flies (Psychodidae) impact human health, acting as vectors of major tropical diseases. Among these, *Anopheles* mosquitoes transmit malaria, filariasis, and arboviruses; *Aedes aegypti* mosquitoes carry dengue fever and the Zika virus; blackflies carry river blindness; sand flies carry leishmaniasis. Other dipterans



The large bee-fly, *Bombylius major*, is a Batesian mimic of bees.

are a nuisance to humans, especially when present in large numbers; these include houseflies, which contaminate food and spread food-borne illnesses; the biting midges and sandflies (Ceratopogonidae) and the houseflies and stable flies (Muscidae).^[34] In tropical regions, eye flies (Chloropidae) which visit the eye in search of fluids can be a nuisance in some seasons.^[95]

Many dipterans serve roles that are useful to humans. Houseflies, blowflies and fungus gnats (Mycetophilidae) are scavengers and aid in decomposition. Robber flies (Asilidae), tachinids (Tachinidae) and dagger flies and balloon flies (Empididae) are predators and parasitoids of other insects, helping to control a variety of pests. Many dipterans such as bee flies (Bombyliidae) and hoverflies (Syrphidae) are pollinators of crop plants.^[34]



An *Anopheles stephensi* mosquito drinking human blood. The species carries malaria.

Uses



Diptera in research: *Drosophila melanogaster* fruit fly larvae being bred in tubes in a genetics laboratory

Drosophila melanogaster, a fruit fly, has long been used as a model organism in research because of the ease with which it can be bred and reared in the laboratory, its small genome, and the fact that many of its genes have counterparts in higher eukaryotes. A large number of genetic studies have been undertaken based on this species; these have had a profound impact on the study of gene expression, gene regulatory mechanisms and mutation. Other studies have investigated physiology, microbial pathogenesis and development among other research topics.^[96] The studies on dipteran relationships by Willi Hennig helped in the development of cladistics, techniques that he applied to morphological characters but now adapted for use with molecular sequences in phylogenetics.^[97]

Maggots found on corpses are useful to forensic entomologists. Maggot species can be identified by their anatomical features and by matching their DNA. Maggots of different species of flies visit corpses and carcasses at fairly well-defined times after the death of the victim, and so do their predators, such as beetles in the family Histeridae. Thus, the presence or absence of particular species provides evidence for the time since death, and sometimes other details such as the place of death, when species are confined to particular habitats such as woodland.^[98]



Blowflies feeding on the fresh corpse of a porcupine, *Hystrrix africae australis*



Maggots used as animal feed at London Zoo

Some species of maggots such as blowfly larvae (gentles) and bluebottle larvae (casters) are bred commercially; they are sold as bait in angling, and as food for carnivorous animals (kept as pets, in zoos, or for research) such as some mammals,^[99] fishes, reptiles, and birds. It has been suggested that fly larvae could be used at a large scale as food for farmed chickens, pigs, and fish. However, consumers are opposed to the inclusion of insects in their food, and the use of insects in animal feed remains illegal in areas such as the European Union.^{[100][101]}

Fly larvae can be used as a biomedical tool for wound care and treatment. Maggot debridement therapy (MDT) is the use of blow fly larvae to remove the dead tissue from wounds, most commonly being amputations. Historically, this has been used for centuries, both intentional and unintentional, on battlefields and in early hospital settings.^[102] Removing the dead tissue promotes cell growth and healthy wound healing. The larvae also have biochemical properties such as antibacterial activity found in their secretions as they feed.^[103] These medicinal maggots are a safe and effective treatment for chronic wounds.^[104]



Casu marzu is a traditional Sardinian sheep milk cheese that contains larvae of the cheese fly, *Piophilidae casei*.

The Sardinian cheese casu marzu is exposed to flies known as cheese skippers such as *Piophilidae casei*, members of the family Piophilidae.^[105] The digestive activities of the fly larvae soften the cheese and modify the aroma as part of the process of maturation. At one time European Union authorities banned sale of the cheese and it was becoming hard to find,^[106] but the ban has been lifted on the grounds that the cheese is a traditional local product made by traditional methods.^[107]

Notes

- a. Some authors draw a distinction in writing the common names of insects. True flies are in their view best written as two words, such as crane fly, robber fly, bee fly, moth fly, and fruit fly. In contrast, common names of non-dipteran insects that have "fly" in their names are written as one word, e.g. butterfly, stonefly, dragonfly, scorpionfly, sawfly, caddisfly, whitefly.^[2] In practice, however, this is a comparatively new convention; especially in older books, names like "saw fly" and "caddis fly", or hyphenated forms such as house-fly and dragon-fly are widely used.^[3] In any case, non-entomologists cannot, in general, be expected to tell dipterans, "true flies", from other insects, so it would be unrealistic to expect rigour in the use of common names. Also, exceptions to this rule occur, such as the hoverfly, which is a true fly, and the Spanish fly, a type of blister beetle.

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